

On the Development and Morphology of the Mandibular and Hyoid Muscles of Mammals.

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With Plates 38-45 and 9 Text-figures.

IN the course of a paper on the morphology of the muscles of the head in Vertebrates published in this Journal two years ago, I gave a short description of those of the mandibular and hyoid segments in the rabbit. There is great difficulty in distinguishing muscle-Anlagen from surrounding mesoblast in the early stages of developing Mammals, and, not quite satisfied with some of the statements made, I have re-investigated the phenomena. The inquiry has been much facilitated by Prof. J. P. Hill, who very kindly lent me sections of *Dasyurus viverrinus*—an animal which is born with two masticatory muscles only and an incudomeckelian joint, and in which the development of typical mammalian muscles and of a squamoso-mandibular joint takes place after birth. These changes can be easily followed, and enable one to interpret the more obscure phenomena occurring in Mammals with a longer intra-uterine development. Other Mammals have also been investigated, viz. pig, rabbit, *Phoca vitulina*, *Halichærus grypus*, *Bradypus marmoratus*, *Dasypus novemcinctus*, *Manis pentadactyla*, *Didelphys aurita*, *Echidna aculeata*, *Ornithorhynchus*.

The first investigator of the development of the masticatory muscles was Reuter, who stated that in the pig their Anlage is first visible in embryos of 16 mm. Nacken-Steisslänge in

the form of an inverted Y, the two limbs of which lie on either side of the lower jaw. The temporal muscle develops from the upper limb, the masseter from the lower external limb, and the two pterygoids from the lower internal limb. He did not mention the tensor tympani or the tensor veli palatini. Eschweiler described the development of the tensor tympani and tensor veli palatini in the pig. He found the first indication of the muscles in embryos of 15.75 mm. Scheitel-Steisslänge, when the masticatory musculature appears in the "Blastensäule" which contains Meckel's cartilage as its nucleus. The Anlagen of the tensor tympani and the malleus portion of Meckel's cartilage form at first an indivisible mass. The differentiation of the muscle-Anlage to muscle occurs in embryos of 20.5 mm. It forms the aboral end of the "Blastensäule," which, orally, forms the masticatory muscles. On the medial side of the Anlage of the masticatory muscles develops the Anlage of the tensor veli palatini; its aboral end is gradually lost in connective tissue, which is continuous, aborally, with the Anlage of the tensor tympani (i. e. the two muscles do not overlap). The Anlage of the tensor tympani shifts aborally, whilst its development into muscle takes place in the reverse direction. In later development the oral end of the tensor veli palatini spreads into the velum, and the tensor tympani gains an attachment to the labyrinth capsule.

Lewis (1910) gave an account of the development of the masticatory muscles in man, which is very similar to that given by Reuter in the pig. The chief point in which he differed is that "in a 14 mm. embryo the Mm. tensor tympani and tensor veli palatini are to be recognised and are connected with the pterygoid mass from which they probably arise."

In the following account of the development of the mandibular and hyoid muscles, those of the mandibular segment are first described and subsequently those of the hyoid segment. On account of the relationship of the anterior digastric to the posterior digastric, it is convenient to consider the depressor mandibulae anterior and anterior digastric

(which are proliferated from the intermandibularis) with the hyoid muscles.

In stage A (just born) of *Dasyurus* (figs. 1 and 2), there is a cartilaginous ala orbitalis, orbito-parietal commissure, and parietal-platte, continuous with one another. The ala temporalis forms a ventro-lateral process of the presphenoid region of the chondrocranium; its free extremity turns forward. There is no line of demarcation between the processus alaris and ala temporalis. The incus is a precartilaginous mass. Meckel's cartilage is a continuous cartilaginous structure, and has not divided into malleus and portion in front. The Anlage of the mandible is a group of cells dorsal to and extending down a little distance on the outside of Meckel's cartilage. In this Anlage, dorso-lateral to Meckel's cartilage, ossification is just visible in the region of attachment of the lateral muscle; anteriorly it is more marked and extends forward almost to the front end of the cartilage. Two masticatory muscles are present, medial and lateral. The medial muscle arises from the ala temporalis; its most anterior fibres pass downwards and outwards to the inner surface of Meckel's cartilage, whilst the succeeding ones pass more and more obliquely backwards to the bar; the hindmost fibres are attached as far backwards as the malleus portion; the fibres form one continuous sheet. The lateral muscle—the front end of which is anterior to that of the medial muscle—arises from the orbito-parietal commissure, passes downwards, and is attached to the upper border of the Anlage of the mandible. Both muscles consist of cross-striated muscle-fibres. The third division of the fifth cranial nerve passes downwards between the two muscles, giving off the ramus medialis to the medial muscle and the ramus lateralis to the lateral muscle. The intermandibularis forms a ventrally curved transverse sheet between Meckel's cartilages; it has a median raphé, and is attached laterally to the inner surface of the cartilage. The mylohyoid nerve passes down on its outer surface.

In stage C (figs. 6 to 11) the medial muscle has separated into anterior and posterior portions. The former is the

internal pterygoid, the latter the common Anlage of the tensor veli palatini and tensor tympani. The internal pterygoid retains its origin from the ala temporalis, whilst the upper end of the Anlage of the tensor veli palatini and tensor tympani has grown inwards beneath the ala temporalis and is attached to the (mammalian) pterygoid bone, which has now developed behind and in continuity with the palatine bone. The coronoid process of the mandible is beginning to form, and the insertion of the lateral muscle has spread down a little on its outer side. Cells proliferated downwards and backwards from the anterior of these muscle-fibres on the outside of the mandible form the beginning of the masseter muscle (fig. 6).

In stage D (figs. 14 to 18) a cartilaginous bar—the processus ascendens alæ temporalis—has appeared, extending from the upper lateral edge of the ala temporalis to the orbito-parietal commissure; it is a cartilaginous thickening of the anterior edge of the membrana obturatoria covering in the spheno-parietal foramen. The Anlage of the tympanic bone has appeared as a straight rod external to the hinder part of Meckel's cartilage; its anterior end is overlapped by the posterior end of the mandible. The origin of the lateral muscle—hitherto confined to the orbito-parietal commissure—has now additionally spread downwards, so that the muscle arises from orbito-parietal commissure, the membrana obturatoria and the processus ascendens. The coronoid process of the mandible has extended further upwards and the inner fibres of the lateral muscle are attached to its medial side. The Anlagen of the squamous and malar bones are formed, and the masseter in part arises from them. The anterior digastric is being proliferated from the hinder part of the intermandibularis.

In stage E (figs. 20 and 21) a condylar process has formed as a slight elevation of the hinder end of the upper edge of the mandible; and the external pterygoid muscle, of which there is no trace in stage D, is differentiated from the lower posterior edge of the lateral muscle. It consists of muscle-

cells which are much smaller in size than those of the rest of the lateral muscle, and is probably proliferated from it, and not formed by change of direction of already existing muscle-fibres. The external pterygoid muscle takes origin from the lower end of the ascending process of the ala temporalis and passes outwards to the condylar process of the mandible. The lower anterior fibres of the lateral muscle, which now forms the temporal, arise from the ascending process in front of the origin of the external pterygoid.

In stage F (figs. 22 and 23) there is a downward and backward growth from about the middle of the tympanic bone. The goniale bone¹ is also formed; it lies dorsal-median to the tympanic bone, between it and Meckel's cartilage; its anterior end extends slightly further forwards than does the tympanic, and its posterior end further back, underlapping the malleus portion. The origin of the temporal muscle has extended backwards so that it additionally arises from the parietal-platte. The common Anlage of the tensor veli palatini and tensor tympani is beginning to separate into those muscles, and the insertion of the latter has shifted down the side of the malleus portion of Meckel's cartilage to its manubrial process. The tensor veli palatini is inserted on the inner side of Meckel's cartilage and does not reach the tympanic bone lying on the other side of Meckel's cartilage. Fig. 39, taken from a 10 mm. specimen of *Didelphys aurita*, shows a little more advanced stage of the same condition.

In stage H (figs. 24-27) the parietal bone is formed outside the orbito-parietal commissure and parietal-platte, and the temporal arises from it.

The alisphenoid bone is formed on the outer and upper sides of the ala temporalis, and upwards round the processus ascendens, which is also involved in the ossification. The bone extends in front of and behind the process. The lower anterior fibres of the temporal, the external pterygoid, and the upper head of the internal pterygoid correspondingly

¹ I use Gaupp's nomenclature. Palmer has recently homologised it with the supra-angular, though without any discussion of Gaupp's views.

arise from this bone, and the upper fibres of the temporal also from the parietal bone. The external pterygoid has two heads, separated from one another by the buccal nerve. The lower portion of the temporal is beginning to be separated off as the zygomatico-mandibularis. The internal pterygoid has become partially separated into two portions, one head—the original one—arising from the alisphenoid bone, the other from the palate bone; the latter head, in stage J, additionally arises from the pterygoid bone. The proximal portion of the tensor tympani, i. e. that attached to the pterygoid bone, has begun to disappear, and the proximal end of the persisting distal portion lies alongside the distal end of the tensor veli palatini which has lost its attachment to Meckel's cartilage. This process continues, so that by stage J (fig. 28) the adjacent ends of the two muscles join end to end, separated only by a tendinous intersection. In stages C to F the proximal end of the tensor veli palatini is, as stated above, attached to the pterygoid bone; in stage H (fig. 26) it has additionally grown inwards below the pterygoid bone (in which a nodule of cartilage—the hamulus—has appeared) into the soft palate; and in stage J a well-marked transverse aponeurosis connects together the inner ends of the muscles of the two sides. A similar process occurs in *Didelphys aurita*.

In stage H there is a cap of dense tissue just above the dorsal end of the condylar process of the lower jaw, and into this the squamous bone is beginning to spread. In stage J the extension of the squamous inwards is more marked, and a split—the joint cavity—is developed in the dense tissue. Cartilage is developed in the condylar process in stage J (fig. 28). The external pterygoid is inserted into the condylar process and its neck in both stages.

In a 8.5 mm. embryo of *Ornithorhynchus* (figs. 29–33) the Anlagen of the incus, Meckel's cartilage, ala temporalis, and processus alaris are present in a precartilaginous condition. Aggregated mesoblast cells connect together the ala temporalis and processus alaris. The Anlage of the mandible is present, dorso-lateral to that of Meckel's cartilage. The

masticatory muscles consist of long striated muscle-cells, in two groups—a medial and lateral. The anterior fibres of the medial muscle descend vertically from just below the ala temporalis towards Meckel's cartilage, those next behind pass downwards and backwards, and the succeeding ones more and more backwards; the hindmost reach as far back as the hind end of Meckel's cartilage; there is no break in the muscle mass. The lateral muscle consists of fibres which, anteriorly, pass towards the upper edge and outer side of the anlage of the mandible; the upper edge of the innermost fibres is close to the ala temporalis, whilst that of the more external fibres is outside the lateral surface of the Gasserian ganglion. The muscle-fibres which dorsally lie behind the hind end of the Anlage of the mandible pass downward and forwards towards its outer surface, and the lower end of this portion of the muscle is not continuous with that of the anterior portion; dorsally, the two portions of the muscle are continuous.

The third division of the fifth nerve passes downwards between the medial and lateral muscles, giving off the lateral and medial rami to the muscles. The buccal nerve penetrates the inner fibres of the lateral muscle.

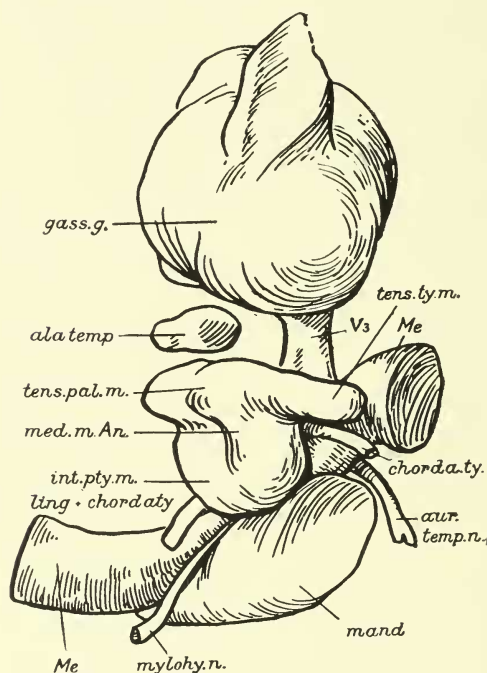
The intermandibularis forms a ventrally curved sheet, attached on each side to the inner surface of Meckel's cartilages. It does not at this stage extend further back. The depressor mandibulæ anterior is being proliferated transversely outwards from the under surface of the intermandibularis.

In a 25 mm. specimen of *Echidna* (= Stage 50 of Semon), the masticatory muscles consist of pterygo-tympanicus, tensor tympani, temporal, external pterygoid, zygomatico-mandibularis, masseter, and detrahens mandibulæ (figs. 34–36). The pterygo-tympanicus arises from the (Mammalian) pterygoid bone and is inserted into Meckel's cartilage. The tensor tympani arises from the (Mammalian) pterygoid bone and is inserted into the malleus portion of Meckel's cartilage. The ramus medialis of the mandibular division of the fifth nerve innervates these two muscles. The detrahens mandi-

bulæ arises from the outer end of the inturned crista parotica and is inserted into the outer surface of the mandible.

The intermandibularis (figs. 34-37) has spread behind the jaw as far back as the stylohyale, its anterior fibres—attached to the inner surface of Meckel's cartilage in stage 47—spread

FIG. 65.



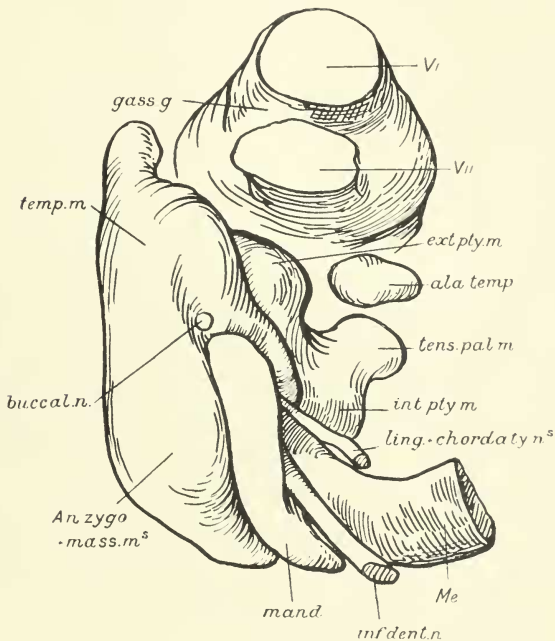
up towards the outer edge of the (Monotreme) pterygoid bone ; the fibres next behind these are attached dorsally to the tympanic bone ; the most posterior fibres are not attached to the stylohyal. The depressor mandibulæ anterior is oblique in position, its inner end is more posterior than its outer, and is attached to dense connective tissue in front of the hyoid ; the fibres pass outwards and forwards and are attached to the inner surface of the mandible.

In a $4\frac{1}{2}$ mm. embryo of the rabbit the Anlagen of the masti-

catory muscles and the intermandibularis are continuous with one another and lie internal to the third division of the fifth nerve; the upper limit of the cell column lies below the Gasserian ganglion.

In a $5\frac{1}{4}$ mm. embryo (fig. 45) the Anlage of the masticatory

FIG. 66.



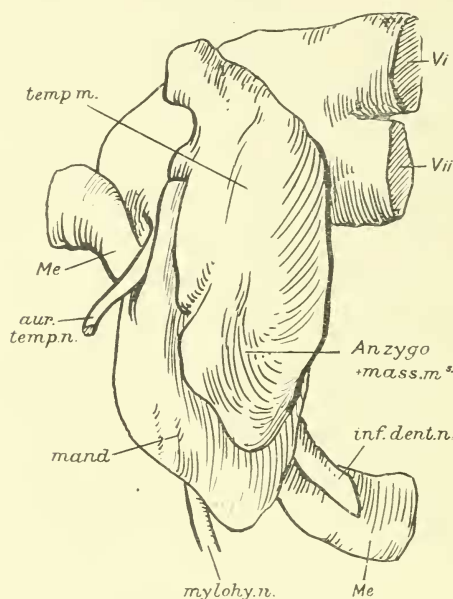
muscles spreads laterally in front of the third division of the fifth nerve, so that the nerve passes down behind the Anlage; whilst the primitive position of nerve and muscle Anlage is preserved lower down in the region of the intermandibularis.

In a 7 mm. embryo the Anlagen of the masticatory muscles and intermandibularis separate from one another. The first branch of the third division of the fifth nerve to be given off is the buccal, which runs forward above the Anlage of the masticatory muscles. The rami medialis and lateralis are formed in an 8 mm. embryo, passing respectively inwards and

outwards into the masticatory Anlage. The ramus posterior is formed in a 9 mm. embryo.

In a 13 mm. rabbit embryo (figs. 65—67) the Gasserian ganglion is a relatively huge mass above the Anlagen of the masticatory muscles. Below the ganglion is the Anlage of the ala temporalis; the processus alaris is not yet formed.

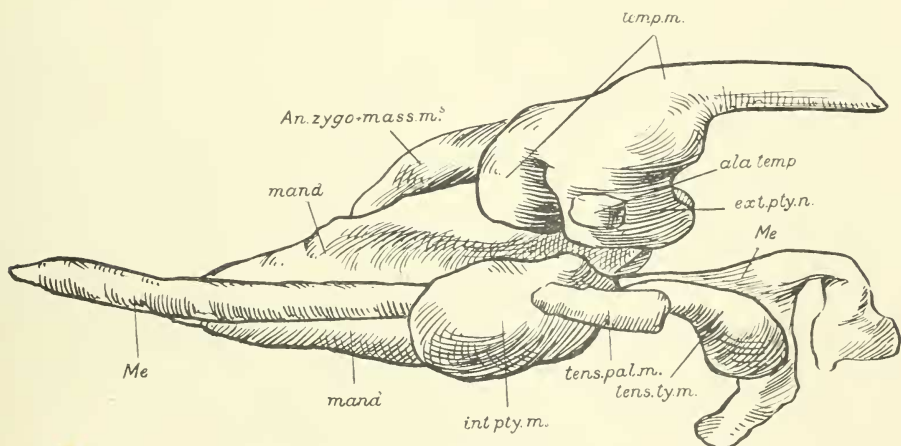
FIG. 67.



Meckel's cartilage is a slightly curved rod. The Anlage of the mandible, in which ossification has not yet begun, lies on the outside of Meckel's cartilage; its anterior edge does not extend quite so far forwards as that of the muscle-Anlagen; posteriorly its upper part ends abruptly except below, where there is a slight backward process. The auriculo-temporal nerve runs outwards and downwards behind the abrupt posterior edge and over the slight backward projection of the mandible. The Anlage of the masticatory muscles has not yet divided into medial and lateral portions, these being

continuous in front of the mandibular division of the fifth nerve. The medial portion extends downwards from just below the ala temporalis inside Meckel's cartilage towards the mandible; there is an inward bulge from its upper part—the Anlage of the tensor veli palatini, and a long posterior projection—the Anlage of the tensor tympani, extending backwards to the malleus; the main mass of the medial portion is the Anlage of the internal pterygoid. The main mass

FIG. 68.

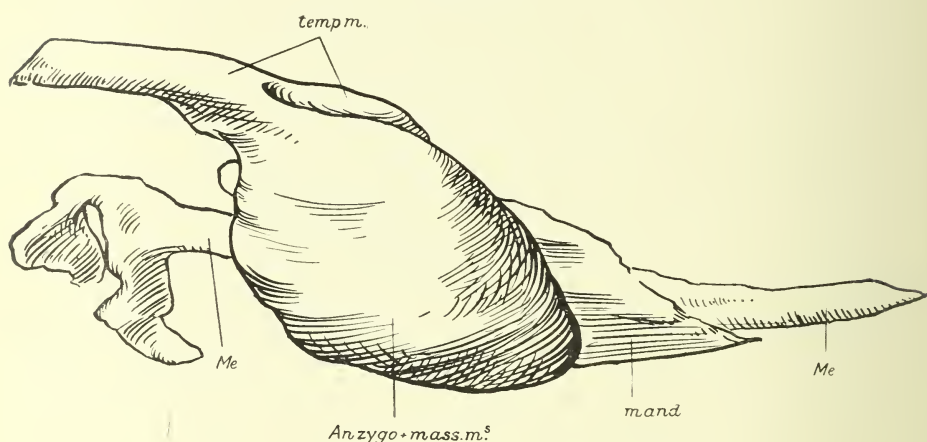


of the lateral portion (Anlage of temporal) has an upward projection on the outer side of the Gasserian ganglion, its lower end embraces the upper part of the mandible. There is a notch on its posterior border—the first indication of the separation of a zygomatico-mandibularis and masseter portion from the temporal, and an inward projection—the Anlage of the external pterygoid, from the hinder part of its inner aspect, towards the ala temporalis.

In a 16 mm. embryo (figs. 46–48 and 68, 69) the ala orbitalis and orbito-parietal commissure, the latter with a free posterior extremity, are present. The parietal-platte and processus alaris are not formed. The ala temporalis has no processus ascendens. The Anlage of the mandible has coronoid and

condylar processes. The Anlage of the masticatory muscles has divided into medial and lateral parts, each of which is imperfectly separated into muscles, which consist of groups of spindle-shaped cells. The medial part consists of the following: the internal pterygoid, which arises from the ala temporalis and is inserted into the mandible, it shows the beginning of a division into two parts. The tensor veli palatini lies just internal to the upper end of the internal

FIG. 69.

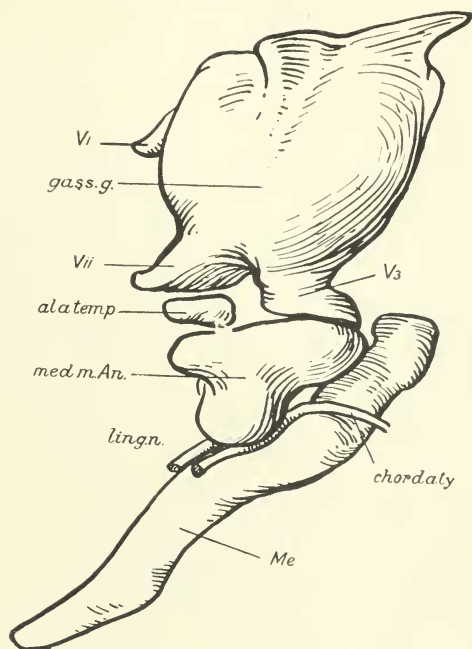


pterygoid with a free anterior end; it passes backwards above the hinder margin of the internal pterygoid and has a free posterior end. The tensor tympani lies immediately above and in contact with the hinder part of the tensor veli palatini, with a free anterior end; it passes backwards and inwards to the side of the malleus. The lateral part of the Anlage of the masticatory muscles consists of the following: the temporal, which has an oblique slightly concave inner edge; its upper extremity extends up outside the Gasserian ganglion, but has no dorsal attachment; it is inserted into the coronoid process. The external pterygoid arises from the ala temporalis behind the anterior fibres of the temporal and is inserted into the condylar process of the Anlage of the

mandible. The zygomatico-mandibularis-masseter is partially marked off from the external fork of the temporal by a groove passing upwards from the posterior edge.

In a 23 mm. embryo (figs. 49-53) the muscles have become quite separate from one another. The internal pterygoid now

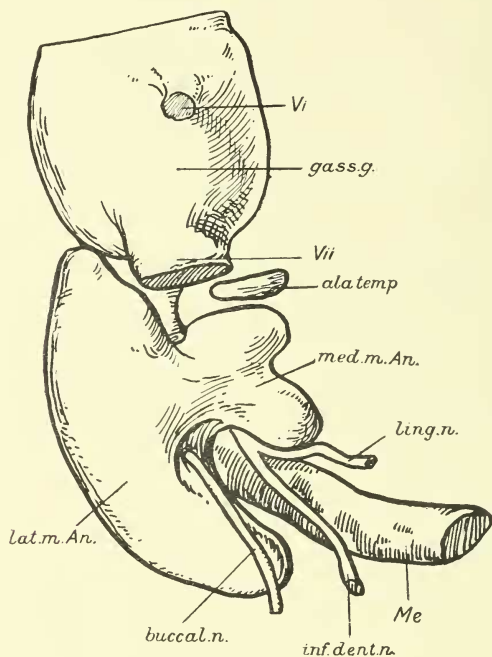
FIG. 70.



arises by two heads, one from the under-surface of the ala temporalis, the other from the palatine portion of the common Anlage of the palate and pterygoid bones; they unite and are inserted into the mandible. The anterior end of the tensor veli palatini winds round the hamulus into the soft palate; the muscle extends backwards medial to the internal pterygoid and is inserted partly to the tympanic bone, partly to the proximal end of the tensor tympani. The tensor tympani now lies wholly behind the internal pterygoid and tensor veli palatini owing to disappearance of its anterior

portion; it arises partly from the tendon of the tensor veli palatini, partly from the outer surface of the auditory capsule. The external pterygoid arises partly from the external surface of the ala temporalis and partly from the palatal portion of the common Anlage of the palate and pterygoid bones. The temporal arises by two heads, from the lamina

FIG. 71.



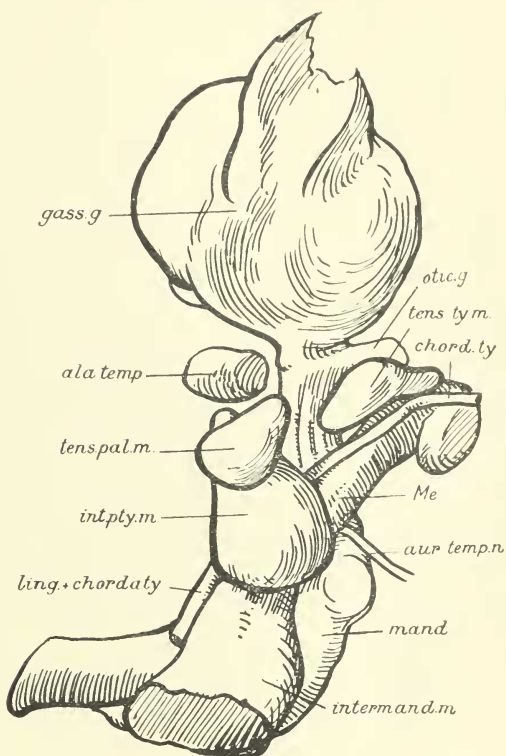
ascendens alæ temporalis and from the Anlage of the parietal bone. The masseter and zygomatico-mandibularis, not yet separated, are continuous dorsally with the temporal.

In a 33 mm. embryo (fig. 54) the zygomatico-mandibularis and masseter have become separated. The palatine and pterygoid bones have ossified, and one head of the external pterygoid arises from the palate bone.

Figs. 70 and 71 represent a model made from sections passing through the Anlage of the masticatory muscles in a

19 mm. embryonic pig ; the stage of development is a little less advanced than a 13 mm. rabbit embryo. Meckel's cartilage is a slightly curved rod of pre-cartilage ; its hinder portion and the Anlage of the mandible, though present, had

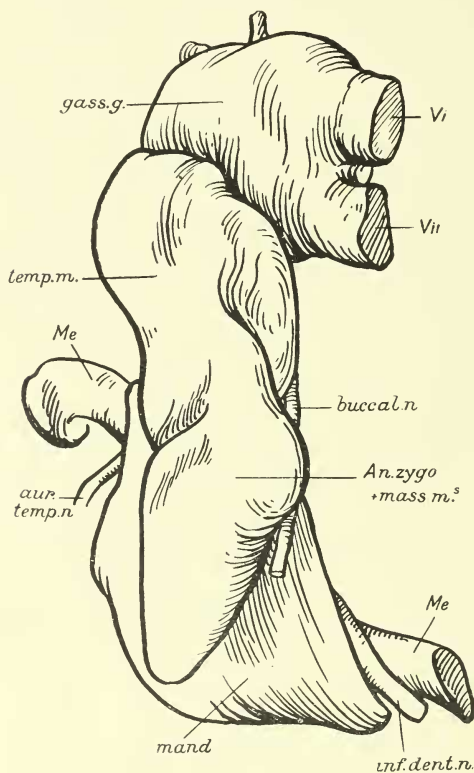
FIG. 72.



not sufficiently clear outlines to be modelled. The Anlage of the ala temporalis is present ; those of the ala orbitalis, orbito-parietal commissure, parietal-platte, and processus alaris, are not yet formed. The Anlage of the masticatory muscles forms a continuous mass, approximately Λ -shaped, with an apex just beneath the ala temporalis, and having an upward projection on the outer side of the Gasserian ganglion. The

outer limb of the mass, with the upward projection, is the Anlage of the temporal, external pterygoid and masseter muscles. The inner limb is the Anlage of the internal pterygoid, tensor veli palatini, and tensor tympani; there is

FIG. 73.



an inward bulge of its upper part—the future tensor veli palatini, and a backward projecting part—the future tensor tympani; its lower end is separated from Meckel's cartilage by the chorda tympani.

The third division of the fifth nerve gives off the buccal nerve (which penetrates the upper part of the outer limb of the mass), then passes down behind the apex of the mass,

giving off the rami medialis and lateralis, and then forwards in the gap between the two limbs, dividing into auriculo-temporal, mylohyoid, inferior dental, and lingual branches.

Figs. 59-63 and 72, 73 are made from a 21 mm. pig embryo. The stage of development of the masticatory muscles is slightly more advanced than that of a 16 mm. rabbit embryo. The ala orbitalis is continuous posteriorly with the orbito-parietal commissure, which does not reach the parietal-plate. The ala temporalis is just beginning to chondrify. The processus alaris is not yet formed. The Anlage of the mandible, in which ossification has not begun, lies outside Meckel's cartilage and shows slightly marked coronoid and condylar processes. The Anlage of the masticatory muscles has divided into medial and lateral portions. The former consists of internal pterygoid, tensor veli palatini and tensor tympani—which are separate structures, though very close together. The internal pterygoid arises from the ala temporalis and is inserted into the mandible, the spindle-shaped cells not having any attachment to Meckel's cartilage. The tensor veli palatini, which is not attached to any skeletal structure, lies internal to the upper end of the internal pterygoid, with its muscle-cells at right angles to those of the internal pterygoid. The tensor tympani lies behind the tensor veli palatini, with a free anterior extremity; it is inserted, posteriorly, into the non-chondrified malleus portion of Meckel's cartilage. The lateral portion of the Anlage of the masticatory muscles consists of temporal external pterygoid, zygomatico-mandibularis, and masseter muscles, which are only partially separated from one another. The temporal has no upper attachment, its lower anterior fibres are in front of the external pterygoid, those above extend upwards outside the Gasserian ganglion; it is inserted into the coronoid process of the mandible. The external pterygoid arises from the ala temporalis and is inserted into the condylar process of the mandible.

The Anlage of the zygomatico-mandibularis and masseter is continuous with the temporal and is inserted into the Anlage of the mandible. The united lingual and inferior dental

nerves pass between the internal and external pterygoids, then separate; the lingual is joined by the chorda tympani medial to the internal pterygoid and passes to the inferior maxillary ganglion; the inferior dental passes forward on the medial surface of the Anlage of the mandible. The mylohyoid branch of the inferior dental passes downwards between Meckel's cartilage and the Anlage of the mandible and then forwards on the lateral surface of the intermandibularis muscle. The auriculo-temporal passes outwards between Meckel's cartilage and the Anlage of the mandible.

In a 24 mm. pig embryo the condyloid and coronoid processes of the mandible are better marked, and ossification has begun. The upper end of the temporal has grown further upwards outside the membranous cranium, but is not attached to the orbito-parietal commissure. The Anlage of the parietal bone is not yet formed. The Anlage of the zygomatico-mandibularis and masseter arises partly from the temporal, partly from the Anlage of the zygomatic arch.

In a 32 mm. embryo (fig. 64), the orbito-parietal commissure is complete; it is covered by the Anlage of the parietal bone. The alisphenoid bone is not yet formed. The temporal arises from the parietal bone and the lamina ascendens ala temporalis which is now formed. The Anlage of the zygomatico-mandibularis and masseter is beginning to separate into those two muscles. The internal pterygoid remains single, arising from the under surface of the ala temporalis. The proximal end of the tensor veli palatini has spread into the soft palate round the hamulus; its distal end is connected with the tensor tympani by a tendinous intersection.

The above-described phenomena show that the Anlage of the masticatory muscles in Mammals divides into medial and lateral portions, and that each develops into certain muscles. These may be taken separately.

Medial Muscle.—The primitive form of the medial muscle is present in 8.5 mm. embryos of *Ornithorhynchus* and stages A and B of *Dasyurus*, taking origin from the ala temporalis and inserted into the whole length of Meckel's

cartilage. This is not present in the rabbit and pig, being passed over in the Anlage stage.

The medial muscle or muscle-Anlage in *Dasyurus*, rabbit and pig, separates into three—from before backward, the internal pterygoid, tensor veli palatini, and tensor tympani. The internal pterygoid is the first to separate, the division into tensor veli palatini and tensor tympani occurring later. The internal pterygoid of *Dasyurus* first forms a muscle passing from the ala temporalis to Meckel's cartilage. On the occurrence of ossification it passes from the alisphenoid bone to the mandible and also gains an additional origin, from the palate and pterygoid bones. This is also the case in *Didelphys aurita*. In the rabbit and pig, the muscle at first arises from the ala temporalis and is inserted into the mandible—the stage of insertion into Meckel's cartilage being passed over. On ossification the muscle arises from the alisphenoid bone, with—in the case of the rabbit—an additional head from the palate bone.

In adult forms of *Ornithorhynchus* and *Echidna* there exists a muscle which was stated by Meckel and by Toldt to be homologous with the internal pterygoid of other mammals. Schulman stated that it is a true member—the caput anterius—of the temporalis group, as shown by its connection with the rest of the muscle and by its innervation by the N. temporalis profundus. This latter statement is confirmed by the evidence of embryos of *Echidna* in Stages 47 and 50 (of Semon); in these there is no muscle arising from the ala temporalis or (Mammalian) pterygoid bone and inserted into Meckel's cartilage or mandible. An internal pterygoid is thus absent.

An 8.5 mm. embryo of *Ornithorhynchus* (fig. 30) shows that the anterior fibres of the median masticatory muscle descend vertically to Meckel's cartilage, i. e. fibres are present homologous with those which form the internal pterygoid in *Dasyurus*. It may be concluded that this muscle atrophies in *Monotremes*, though whether its development in *Ornithorhynchus* advances a stage further than that just mentioned

before it atrophies could not be determined owing to want of material.

The pterygo-tympanicus s. tensor veli palatini is the middle one of the three into which the primitive medial muscle or muscle-Anlage separates.

Its development could not be followed in Ornithorhynchus. In Echidna—stage 50, the earliest available—the pterygo-tympanicus arises from the (Mammalian) pterygoid bone and is inserted into Meckel's cartilage. The muscle subsequently disappears, being absent in the adult (Schulmann).

In Dasyurus the pterygo-tympanicus arises from the pterygoid bone and is inserted into Meckel's cartilage, there being no stage in which, as a separate muscle, it arises from the ala temporalis. In later stages the distal end of the muscle loses its attachment to Meckel's cartilage and becomes connected with the persisting distal end of the tensor tympani. Insertion into the tympanic bone does not occur. At the same time the proximal end of the muscle—hitherto attached to the pterygoid bone—additionally grows inwards in the soft palate and forms an aponeurosis with the muscle of the opposite side. The pterygo-tympanicus thus becomes the tensor veli palatini. The same series of events occurs in Didelphys aurita.

In the rabbit the pterygo-tympanicus s. tensor veli palatini, when first visible as a separate muscle, lies on the medial side of the internal pterygoid. Its proximal end does not gain any attachment to the ala temporalis or pterygoid bone, but, later, grows inward in the soft palate round the hamulus. Its distal end becomes attached to the tympanic bone, but there is no antecedent stage comparable to that of Echidna and Dasyurus in which it is inserted into Meckel's cartilage. It also becomes attached to the persisting distal end of the tensor tympani. In the pig the process of development is abbreviated. The muscle, as in the rabbit, is first visible on the medial side of the internal pterygoid; its proximal end does not gain any attachment to either the ala temporalis or

pterygoid bone, but grows round the hamulus into the soft palate; its distal end does not gain any insertion to either Meckel's cartilage or the tympanic bone, but becomes attached to the tensor tympani by tendon. In *Dasyurus*, *Didelphys*, rabbit and pig, the development of the hamulus is synchronous with the ingrowth of the muscle into the soft palate.

On comparison of the descriptions of the pterygo-tympanicus given by Kostanecki, Schulman and Lubosch, those of the tensor veli palatini given by Kostanecki, and the embryological phenomena described above, it may be concluded that the muscle is derived from one taking origin from the ala temporalis and inserted into Meckel's cartilage. This stage is not present in any of the animals investigated, but its existence, in phylogeny, may be inferred from the phenomena in early stages of *Ornithorhynchus* and *Dasyurus*, i.e. an undivided medial muscle passing from the ala temporalis to Meckel's cartilage, and after separation of this into parts, the insertion of the pterygo-tympanicus, in *Echidna* and *Dasyurus*, into Meckel's cartilage.

On the occurrence of ossification the muscle extended from the (Mammalian) pterygoid bone to the tympanic bone. In *Dasyurus* this stage is present as regards the origin of the muscle but insertion into the tympanic bone is passed over; in the rabbit it is present as regards the insertion but passed over as regards the origin; in the pig neither attachment occurs.

The Anlage of the tympanic bone in *Dasyurus* is formed as a straight rod ventro-lateral to the hinder part of Meckel's cartilage, with its anterior part overlapped by the Anlage of the mandible; subsequently an outgrowth downwards and backwards occurs, originating just behind the hind edge of the mandible. This method of formation is in harmony with the theory of van Kampen that the tympanic bone was primarily a covering bone for the hinder part of Meckel's cartilage, and only subsequently—on development of a squamoso-mandibular jaw joint—became a part of the wall of the tympanic cavity. He suggested that it was derived from the supra-angularis or

angulare of the lower jaw, which are present in Amphibia and Reptiles. This opinion was adopted by Gaupp, who homologised the tympanic bone with the angulare, and pointed out that the presence of a pterygo-tympanicus in some Mammals was an additional fact in favour of van Kampen's theory.

It is probable, then, that the muscle—on the occurrence of ossification—arose from the (Mammalian) pterygoid bone, and was inserted into the meckelian (perhaps the only) portion of a tympanic bone which formed a covering bone for the old jaw with an incudo-meckelian joint. On the development of the new squamoso-mandibular joint, the muscle, being inserted behind this point, lost its significance as regards any action on the jaw, and as far as present information goes, this condition is not preserved in any adult Mammal.

No young enough Edentate embryos have been investigated to ascertain whether, in ontogenetic development, the muscle is inserted into the meckelian portion of the tympanic bone, but an indication of at least its phylogenetic existence is given by the temporary insertion of the muscle in *Dasyurus* into Meckel's cartilage opposite this portion of the bone. In late embryos of *Dasyurus novemcincta* and *Bradypus mar-moratus* the muscle is inserted into the later formed lower limb of the bone.

Insertion solely into the tympanic bone is preserved to the adult condition in *Bradypus tridactylus*; the muscle generally spreads to neighbouring structures. Thus Schulman described its insertion in *Ornithorhynchus* to the junction of the os sphenoides and os petrosus, in *Choloepus* to the ligamentum accessorium mediale and walls of the fissura squamoso-petro-tympanica, in *Manis* to the "Trommelhöhle," in *Tamandua* to the bone round the cleft through which the chorda tympani passes; and Kostanecki described the insertion in *Dasyurus sexcinctus* to the bulla tympanica and os sphenoides.

The origin of the pterygo-tympanicus from the pterygoid bone is, similarly, rarely preserved; in Edentates only, as far as present information goes, in *Tamandua* (Schulman),

Tolypeutes (Lubosch), *Bradypus tridactylus* (Kostanecki) *Manis pentadactyla* (F. H. E.), whereas in *Choloepus* and *Manis Javanica* (Schulman), *Dasypus sexcinctus* (Kostanecki), *Dasypus novemcincta* and *Bradypus marmoratus* (F. H. E.) the muscle spreads into the soft palate, forming a *tensor veli palatini*.¹ This secondary ingrowth remains in connection with the original pterygo-tympanicus, and may or may not have fibres taking origin from the pterygoid bone.

The condition present in the latter four Edentates hardly differs—as far as regards the proximal portion of the muscle—from that present in higher Mammals where the whole muscle, i. e. pterygo-tympanicus + its ingrowth into the soft palate, has generally been called the *tensor veli palatini*.

Schulman was of opinion that the relations of the pterygo-spinosus s. tympanicus of *Ornithorhynchus* indicated the existence of a movable (Monotreme) pterygoid in *Pro-mammalia*. In *Echidna*, however, the pterygo-tympanicus arises from the (Mammalian) pterygoid in stage 50 (though subsequently atrophying)—an occurrence that suggests that the origin of the muscle in the adult *Ornithorhynchus* from the (Monotreme) pterygoid is a secondary occurrence. Further, adoption of van Kampen's theory that the tympanic bone was, phylogenetically, a covering bone for a jaw with an incudo-meckelian joint, and so a movable structure, makes the theory improbable.

Lubosch doubted the homology of the pterygoid bone in the *Zenarthra* and *Pholidota* with that of other Mammals, and suggested that it might be homologous with the *Echidna* pterygoid, or possibly the result of fusion of a Mammalian with an *Echidna* pterygoid. The early stages are not yet known, but in *Dasypus novemcincta* (embryo 30 mm.) and *Bradypus marmoratus* (embryo 30 mm.) the relations of the pterygo-tympanicus muscle to that bone were identical with those in *Dasyurus*, and the bone, which showed no

¹ Schulman was the first to recognise the genetic relationship between the pterygo-tympanicus and the *tensor veli palatini*.

evidence of fusion, lay ventro-median and close to the ala temporalis, and was apparently homologous with the ordinary Mammalian pterygoid.

The attachment of the (original) proximal¹ end of the tensor veli palatini to the pterygoid bone and hamulus is preserved in Man, Primates, Pinnipedia, Insectivora, Perissodactyla, Artiodactyla, Marsupials; or it may altogether fail as in Cheiroptera, Carnivora, and Rodents (Kostanecki). The embryological phenomena in the rabbit and pig show that the latter occurrence may, at any rate in some cases, be due to its non-development.

The distal end of the tensor veli palatini in the rabbit becomes attached to the tympanic bone, whereas in *Dasyurus*, *Didelphys* and pig this ancient attachment is never gained. In the rabbit it persists up to the stage of 33 mm. (the oldest investigated), but judging from the account given by Kostanecki it is not present in any adult Mammal. It has yet to be determined in what orders other than Rodents a temporary attachment to the tympanic bone is gained. A secondary attachment to other adjacent bones is gained in some orders, e. g. to the bulla ossea in Marsupials and Rodents.

One almost constant feature of the distal end of the tensor veli palatini is attachment to the tensor tympani. Thus Kostanecki states that "Der Zusammenhang zwischen dem Tensor veli und Tensor tympani ist bei vielen Säugethieren erhalten, wo aber ein solcher verloren gegangen ist, weisen doch manche Punkte auf die früher bestehenden Beziehungen hin, die so sogar nur im Anschluss daran erklären lassen." The developmental phenomena in *Dasyurus*, pig and rabbit, show that this connection with the tensor tympani is intimately related to the atrophy or want of development of the proximal portion of the latter muscle.

¹ The nomenclature adopted here is in reference to the original form and attachments of the pterygo-tympanicus, from which the tensor veli palatini is derived, and is the reverse of that used by Kostanecki. The tensor veli palatini is an interesting instance of transference of "origin" from the proximal end to the distal end of a muscle.

The distal end of the tensor veli palatini also gains attachment to the walls of the Eustachian tube, with which it is from the very first in close relationship.

As regards innervation, Schulman determined that the pterygo-spinosus of *Ornithorhynchus* is innervated by a branch of the ramus medialis, s. ventralis, of the mandibular division of the fifth. Lubosch did not describe the innervation of the pterygo-tympanicus of Edentates; but in *Echidna*, *Dasypus novemcincta*, *Bradypus marmoratus*, and *Manis pentadactyla*, I found the same innervation as in *Ornithorhynchus*.

The tensor veli palatini has long been recognised as being innervated by the ramus medialis of the mandibular division of the fifth. I have recently confirmed this by showing that in *Macacus cynomolgus* the muscle degenerates after section of the fifth nerve proximal to the Gasserian ganglion.

Tensor Tympani.—The tensor tympani in early stages of *Dasypus* passes from the pterygoid bone to the side of the body of the malleus portion of Meckel's cartilage. Later on the proximal portion of the muscle disappears, and the proximal end of the persisting distal portion becomes attached to the distal end of the tensor veli palatini and the cartilaginous wall of the auditory capsule. It may be inferred that a stage has been passed over in which the tensor tympani—as a separate muscle—arose from the ala temporalis. Such a stage is present in a 30 mm., i. e. relatively late embryo of *Dasypus novemcincta*.

In *Echidna*, in stage 50, the tensor tympani passes from the (Mammalian) pterygoid bone to the malleus. The proximal portion of the muscle subsequently disappears, the proximal end of the persisting distal portion being attached in the adult to the petrous bone (Eschweiler).

In the rabbit the muscle never has any origin from either the ala temporalis or the pterygoid bone, though a subsequently atrophying, proximal portion of the muscle, overlapping the tensor veli palatini, is formed. The proximal end of the

persisting distal portion becomes attached to the tensor veli palatini by tendon.

In the pig such a proximal portion is not formed; only the persisting distal portion, behind the Anlage of the tensor veli palatini, is developed, as found by Eschweiler. All trace is thus lost, even in developmental stages, of the ancient origin from the pterygoid bone.

It may be concluded, from the descriptions given by Zuckerkandl, Kostanecki, Schulman, and Eschweiler, that the tensor tympani does not arise from the (Mammalian) pterygoid bone in any adult mammal. This may be due to loss of such attachment during development, e. g. in *Echidna*, *Dasyurus*, *Bradypus marmoratus*, or to its non-formation, e. g. rabbit and pig.

Disappearance of the proximal portion of the muscle either by ontogenetic atrophy or by non-formation is a marked characteristic of the muscle. In the former case it is apparently brought about by the bulging wall of the pars cochlearis of the auditory capsule interrupting the line of action of the muscle. The proximal end of the persisting, or solely developed, distal portion of the muscle gains secondary attachments, and especially to the pars cochlearis of the auditory capsule and Eustachian tube. Of these attachments that to the Eustachian tube is in close association with the secondary insertion of the tensor veli palatini, as described above.

Eschweiler was of the opinion that these various attachments of the tensor tympani are derived from the condition found in *Ornithorhynchus*, where the muscle in the adult consists of two parts, both inserted into the malleus—a “Rachenbauch” which takes origin from “der Muskulatur hervor welche am hintern lateralen Choanenwand entspringt,” and a “Felsenbeinbauch” springing from the labyrinth wall.

The development of the muscle in *Ornithorhynchus* is not yet known, but comparison with *Echidna*, *Dasyurus*, pig and rabbit leads to the conclusion that in all probability the “Rachenbauch” of *Ornithorhynchus* is a secondary formation.

Temporal.—In *Dasyurus* the first origin of the lateral masticatory muscle (from which the temporal, masseter, zygomatico-mandibularis and external pterygoid are subsequently formed) is from the orbito-parietal commissure; the dorsal attachment of the muscle then spreads backwards to the parietal-platte and downwards to the membrana obturatoria covering in the spheno-parietal foramen, with its front edge to the lamina ascendens of the ala temporalis. On the occurrence of ossification the temporal muscle, which has been formed owing to the differentiation of the lateral group muscles, arises from the parietal and alisphenoid bones, the former being developed over the orbito-parietal commissure and parietal-platte, the latter over the ala temporalis, lamina ascendens and the membrana obturatoria.

In the rabbit and pig, with a longer intra-uterine development, the Anlage of the lateral masticatory muscle separates into the muscles it forms before attachment takes place. The temporal becomes attached to the lamina ascendens alæ temporalis, and spreads upwards to the territory of the orbito-parietal commissure and parietal-platte, but these latter structures are by that time covered by the Anlage of the parietal bone from which the muscle gains an origin. On the subsequent ossification of the alisphenoid bone the lower fibres arise from that bone.

The lamina ascendens alæ temporalis is complete in *Dasyurus* and *Didelphys aurita*; it has a free upper end in rabbit, pig, and *Dasypus*. The orbito-parietal commissure is complete in all four animals.

The lower end of the lateral masticatory muscle in the just born *Dasyurus* is at first attached to the upper edge of Meckel's cartilage via a mass of cells in which the Anlage of the mandible is just visible. Ossification subsequently extends upwards forming a coronoid process and downwards on the lateral side of Meckel's cartilage; in relation with these changes the insertion of the muscle becomes forked and laps the coronoid process on both sides, though to a greater extent laterally than medially.

In the rabbit and pig there is no stage in which the temporal muscle is inserted solely into the upper edge of the Anlage of the mandible; its cells become spindle-shaped before it spreads downwards, with a forked extremity, on either side of the Anlage of the mandible.

The formation of the coronoid process of the mandible takes place in *Dasyurus* after ossification has begun, in the rabbit and pig in the Anlage stage. In all three animals the process is formed by a dorsal extension into an already formed muscle or muscle-Anlage.

The stages of *Ornithorhynchus* and *Echidna* available did not permit of observations on the development of the individual muscles formed from the lateral masticatory muscle.

Masseter and Zygomatico-mandibularis.—In many Mammals a zygomatico-mandibularis is differentiated between the temporal and masseter muscles. Allen, who first described the muscle, in man, considered it to be a separated deep portion of the masseter, whilst Toldt held that it is derived from the temporal. Toldt stated that “er stammt von der Muskelfasergruppe her, welche die oberflächlichste Schichte der ursprünglichen Anlage des Schläfenmuskels darstellt und von jener Mesodermischiechte kommt welche sich bleibend zur Fascia temporalis gestaltet. Da sich in derselben Mesodermischiechte später das Jochbein, beziehungsweise der ganze Jochbogen entwickelt, so tritt ein bestimmter Anteil der bezeichneten Fasergruppe mit der medialen Fläche des Jochbogens in Beziehung, d. h. er nimmt von dieser bis an ihren unteren Rand herab bleibend seinen Ursprung. Er steht demgemäss an seinen Ursprung mit dem Schläfenmuskel in ununterbrochenen Zusammenhang, hat aber durch die erworbene Beziehung zum Jochbogen einen besonderen Character erlangt.”

In *Dasyurus*, as detailed above, the masseter muscle is proliferated, in stage C, downwards and backwards from the anterior ventral edge of the lateral muscle on the outside of the mandible; and from that time onward can be distinguished in transverse section by the direction of its fibres. The

zygomatico-mandibularis is formed subsequently, in stage H, by a separation of the ventral fibres of the temporal muscle, dorso-posterior to the masseter muscle. The fibres of the zygomatico-mandibularis have the same direction as those of the temporal, and up to stage J—the latest investigated—the separation was not complete.

In the rabbit and pig the process is a little different. The Anlage of the lateral masticatory muscle is inserted by a forked lower edge into the mandible. A groove appears in the posterior edge of the external fork, and spreading upwards and forwards separates the common Anlage of the masseter and zygomatico-mandibularis from the temporal. This Anlage divides into masseter and zygomatico-mandibularis, the latter being cut off from the upper posterior part of the common mass. In view of the many modifications associated with the prolonged intra-uterine development, it is probable that the phenomena occurring in *Dasyurus* more closely represent the phylogenetic history of the muscles than do those of the rabbit and pig. Both masseter and zygomatico-mandibularis have their first insertion into the Anlage of the mandible. Neither has any temporary insertion into Meckel's cartilage.

The *detrahens mandibulæ* is present only in *Monotremes*. No trace of it was seen in the developmental stages of *Dasyurus*, pig and rabbit. It is innervated by the fifth nerve (Westling, Fürbringer, Gaupp, Schulman). Schulman regarded it as belonging to the dorsal (in this paper regarded as "lateral") group of masticatory muscles as—like the temporal, external pterygoid, masseter, and zygomatico-mandibularis—he found it to be supplied by the dorsal s. lateral division of the mandibular nerve.

Owing to want of material its development could not be completely followed in either *Ornithorhynchus* or *Echidna*, but the stages described above permit of an approximate account. The muscle can be identified with the hinder fibres of the lateral masticatory muscle in 8.5 mm. embryos of *Ornithorhynchus*—those fibres which pass downwards and forwards towards the outer surface of the hind end of the Anlage of

the mandible. In stage 47 of *Echidna* the muscle has separated off and passes from the root of the crista parotica downwards and forwards to the outer surface of the mandible. This condition is also present in stage 50. In the adult *Echidna* this primary origin is lost, and the muscle arises from the ventral surface of the squamosal bone (Schulman).

These phenomena support the view of Schulman that the *detrahens mandibulæ* is one of the lateral group of masticatory muscles. They negative the view of Toldt that it is split off from an already differentiated masseter, and suggest that the muscle is, phylogenetically, more ancient than either the masseter, *zygomatiko-mandibularis* or external pterygoid.

The external pterygoid muscle is developed from the temporal in *Dasyurus*, pig and rabbit. Its origin in *Ornithorhynchus* and *Echidna* was not determined owing to a want of the necessary stages. The process could be most clearly seen in *Dasyurus*, where the cells forming the muscle are at first small and non-striated, and probably proliferated from, and not formed by change of direction of, the longer cross-striated muscle cells of the temporal. In the rabbit and pig the formation of the external pterygoid takes place in an *Anlage* consisting of oval cells, and appeared to be due to separation of a portion of the temporal *Anlage*.

The primary origin of the external pterygoid in *Echidna* is from the *membrana obturatoria* above the *ala temporalis*; in *Dasyurus*, and *Didelphys aurita* it is from the lower end of the *lamina ascendens alæ temporalis*; in the rabbit and pig from the *ala temporalis*. On the formation of the alisphenoid bone outside the *ala* and its *lamina ascendens*, the muscle—in *Dasyurus*, *Didelphys*, rabbit and pig—arises from this bone; and in the rabbit it gains an additional origin from the palate bone. In the adult *Echidna* (Schulman) the muscle arises from the *planum infratemporale* of the great wing of the sphenoid and from the *ala temporalis palatini*.

Origin of the muscle from the alisphenoid bone is common: thus Lubosch describes the origin of the muscle, in *Bradypus* from the pterygoid bone, in *Dasypus* and *Tolypeutes* by

two heads from the alisphenoid, in *Tatusia* by two heads, one from the alisphenoid, the other from the alisphenoid and palate bones, in *Tamandua* by two heads, one from the parietal, the other from the palate.

The first insertion of the external pterygoid is into the condylar process of either the ossified mandible (*Dasyurus*) or its *Anlage* (rabbit and pig). There is no transitory insertion into Meckel's cartilage. The development of a condylar process is synchronous with the development of the external pterygoid. These phenomena support the view of Gaupp that the condylar process is primarily a "Muskelfortsatz."

An external pterygoid muscle is present in most Mammals. Two exceptions have been recorded and are of considerable interest. Leche was of opinion that the internal and external pterygoid muscles "auf einen gemeinsamen Ursprung zurückgeführt werden können," but did not record any instances other than that of *Phoca*, in which one muscle only was present, which might represent a common muscle mass from which in other Mammals internal and external pterygoids were differentiated.

Humphry had described in *Phoca communis* one pterygoid muscle only "arising from the outer side and edge of the slightly developed pterygoid part of the sphenoid and passing to the inner side of the angular part of the jaw." He did not mention its innervation nor did he describe the temporal muscle.

I find that in *Halichærus grypus* (grey seal) the masseter, zygomatico-mandibularis, temporal, external pterygoid, internal pterygoid, tensor veli palatini and tensor tympani muscles are present. The temporal is inserted into the coronoid process, the external pterygoid into the condyloid process and interarticular meniscus, and the internal pterygoid into the inner side of the angular part of the jaw. The ramus lateralis of the mandibular division of the trigeminal nerve supplies the masseter, zygomatico-mandibularis, temporal (by three twigs), and the external pterygoid; the ramus medialis supplies the internal pterygoid, tensor veli palatini, and tensor tympani.

In *Phoca communis* s. *vitulina* (common seal) there is one pterygoid muscle only, as described by Humphry; it agrees in form, origin, insertion and innervation from the ramus medialis, with the internal pterygoid of *Halichærus*. The "temporal" is inserted into the interarticular meniscus, the neck of the condyloid process and the coronoid process (fig. 44); it is innervated by four twigs from the ramus lateralis.

It is clear that the "temporal" of *Phoca* represents the temporal + external pterygoid of *Halichærus*, and the condition is probably due to non-separation of these two muscles—a persistence of an embryonic stage.

The matter, however, is complicated by the statement of Toldt that in *Phoca vitulina* both pterygoid muscles exist—a statement which does not agree with the findings of Humphry and myself in *Phoca vitulina*, though it does agree with what I found in *Halichærus grypus*.

In *Manis tetradactyla*, according to Lubosch, there is only one pterygoid muscle arising from the palate bone and passing down internal to the N. mandibularis. No separate external pterygoid was found. Lubosch was of the opinion that "er mit dem inneren Flügelmuskel verschmolzen ist, und ich beziehe die occipitalsten Fasern seiner Ansatzes, die in der Figur an den Condylus tretend gezeichnet sind, auf ihn." I found a similar condition in *Manis pentadactyla*.

The above-described observations show that the Anlage of the masticatory muscles in Mammals divides into medial and lateral portions. From the medial portion or muscle are developed the internal pterygoid, pterygo-tympanicus or tensor veli palatini, and the tensor tympani. From the lateral portion or muscle are developed the temporal, masseter, zygomatico-mandibularis, and external pterygoid.

These phenomena of development are in harmony with, and offer an explanation of, the method of innervation by the mandibular division of the fifth nerve. The muscles developed from the medial portion are innervated by the ramus medialis, those developed from the lateral portion by the ramus lateralis.

The division of the muscles and nerve-branches into medial and lateral groups is further evidenced, as I have recently shown, by the differing paths of the nerve-fibres—both motor and sensory—into the rami. The fibres of the ramus lateralis have a simple direct path, whilst the fibres of the ramus medialis are for a space split into two parts by the ramus posterior.¹ Both rami contain motor fibres from the motor root, and muscle-sensory fibres from the Gasserian ganglion.

The division is also corroborated by the grouping of the cells in the motor nucleus of the trigeminal nerve. Willems found three groups of cells in this nucleus² in the rabbit—a dorsal, a ventro-median, and a ventro-lateral. The occurrence of chromolytic changes after avulsion of individual motor branches showed that the external pterygoid, the temporal and sphenoidal,³ and the masseter, are innervated by the dorsal group, the internal pterygoid by the ventro-lateral group, the mylohyoid and the anterior digastric by the ventro-median group. No chromolytic changes were found after avulsion of the tensor tympani, and no operations were performed on the tensor veli palatini.

Willems was of the opinion that “ces groupements cellulaires répondent relativement bien à des fonctions différentes.” The internal pterygoid, however, is more closely associated in function with the temporal and masseter than is the external pterygoid. The grouping agrees with the division of their *Anlage* into lateral and medial masticatory muscles or muscle-*Anlagen* during development, and is a morphological one—probably dating from a period antecedent

¹ I showed this to be the case in Man, Macacus, dog, and rabbit. I can now also add *Dasyurus*, *Ornithorhynchus*, and *Echidna*.

² Willems applied the term “masticatory nucleus” to the whole of the motor nucleus of the trigeminus. In this paper the term “masticatory” is used—as is usual in English text-books—to denote those muscles innervated by the fifth cranial nerve which are situated dorsal to the lower jaw, i. e. to the exclusion of the mylohyoid and anterior digastric, with a similar restriction in the case of the parts of the motor nucleus.

³ The part of the temporal innervated by the anterior deep temporal nerve.

to the differentiation of the individual muscles which characterise Mammals. Similarly, the ventro-median group probably dates from a period antecedent to the differentiation of a depressor mandibulæ anterior s. anterior digastric from the intermandibularis.

The buccal nerve is generally described as a branch of the ramus lateralis, alongside of which it runs for a short distance in the adult. It would be preferable, however, in view of its earlier development and different function, to describe it as a separate branch of the mandibular division of the fifth nerve, and to restrict the term "ramus lateralis" to the muscular branch.

The intermandibularis in early stages of *Ornithorhynchus*, *Dasyurus*, rabbit and pig forms a ventrally curved muscular sheet, with a median raphe, and attached laterally to the inner surface of Meckel's cartilage. At a late stage, in *Dasyurus*, pig and rabbit, it becomes attached to the mandible. In *Ornithorhynchus* (Schulman) the muscle is attached laterally to the lower jaw, ligamentum pterygo-mandibulare, os pterygoideum and annulus tympanicus, the last-mentioned portion forming a separate muscle, the tympanico-hyoideus. In *Echidna*, stage 47, the muscle has already extended backward, but its anterior part is still attached to Meckel's cartilage; in stage 50 this attachment is lost and the fibres extend up towards the outer edge of the (Monotreme) pterygoid bone; the fibres behind are attached to the tympanic bone. In the adult (Schulman) the muscle is attached to a fascial sheet at the level of the foramen rotundum, the hinder half of the outer edge of the os palatinum, the os pterygoideum, the ligamentum pterygo-mandibulare, the tympanicum and the stylohyal. The above mentioned embryological phenomena support his view that the absence of attachment of the muscle to the jaw is a secondary occurrence.

On the Homologies between the Masticatory Muscles of Mammals and Non-mammals.—The embryological evidence detailed above suggests that Mammals have originated from forms characterised by two masticatory

muscles only: a medial arising from the ala temporalis and inserted into Meckel's cartilage and innervated by the ramus medialis of the mandibular division of the fifth nerve, and a lateral arising from the orbito-parietal commissure and inserted into a rudimentary mandible and innervated by the ramus lateralis.

In Sauropsida¹ the Anlage of the masticatory muscles divides into upper and lower portions, the former inserted into the palatine process of the quadrate, the latter extending from the palatine process of the quadrate to Meckel's cartilage. The upper portion forms the spheno-ptyergo-quadratus or a homologue of this muscle, or—as in Chelonia and Crocodilia—atrophies. The lower portion of the Anlage of the masticatory muscles separates into inner and outer parts, the inner developing into the pterygoid muscle or muscles, and the outer into the capiti-mandibularis. The dorsal end of the capiti-mandibularis, at first attached to the palato-quadrates, grows upwards and gains a dorsal attachment to the skull.

Thus, whilst in Mammals the Anlage of the masticatory muscles does not divide into upper and lower portions, in Sauropsida it does so. This cardinal difference is not taken into account by Fürbringer, Kostanecki, Gaupp, and Cords, so that the various homologies which they regard as existing between individual masticatory muscles in these two great Vertebrate groups are questionable.

In Amphibia the Anlage of the masticatory muscle does not divide into upper and lower portions, above and below the palatine process of the quadrate. The whole dorso-ventral strip separates into a medial and a lateral muscle.

The initial stages of development of the masticatory muscles in Mammals are thus exactly comparable to those of

¹ Only the barest outline of the phenomena is stated here. In the 'Quarterly Journal of Microscopical Science,' vol. 51, 1907, I gave a short account, in all groups of the Sauropsida, with an analysis of the somewhat bewildering array of names given to the muscles by various observers.

Amphibia, and a distinct homology exists between the medial and lateral masticatory muscles in the two Vertebrate groups. In Mammals these two muscles undergo considerable changes as detailed above, so that no homology exists between any one Mammalian masticatory muscle and any one Amphibian muscle.

The intermandibularis is homologous with the similarly named muscle in other Vertebrate groups, Elasmobranchs, Teleostomi, Amphibia and Sauropsida. Its development in mammals, just as in other Vertebrates, lends no support to the theory of Ruge that it is primarily a hyoid muscle.

As will be shown later (pp. 579, 613, 616), the depressor mandibularis anterior of *Ornithorhynchus* and the anterior digastric of *Dasyurus*, rabbit and pig, are formed by proliferation from the ventral surface of the intermandibularis. There are no homologies in other Vertebrate groups, so that the muscle must have arisen within the Mammalian phylum.

On the Changes in the Jaw Muscles accompanying the Development of the Squamoso-mandibular Joint in Mammals.—*Dasyurus* and *Echidna* are born at an early stage with a functional incudo-meckelian joint, and the change of jaw-joint occurs during the pouch stage of existence.

In the earlier stages of *Dasyurus* the prominent feature is the great development of the lingual muscles—the genio-glossus, hyo-glossus, stylo-glossus, and transverse lingual muscle-fibres; this and the concavity of the anterior part of the dorsal surface of the tongue are intimately associated with the intrabuccal position of the maternal teat. Then follows the development of two new muscles—the transversely directed anterior digastric, which soon, however, becomes more oblique in position, with its medial end attached to the transverse aponeurosis of the hyoid ventral constrictor, and the external pterygoid. The adjacent ends of the genio-hyoid, sterno-hyoid and omo-hyoid lose their attachment to the first branchial cartilage and become united by tendon. These muscle phenomena precede and apparently initiate the development of the squamoso-mandibular joint. In *Phascolarctos*, however,

the genio-hyoid retains its attachment to the basibranchial, and in *Didelphys aurita* the hyoglossus is attached to the first branchial bar. In *Echidna*,¹ where there is no mammary teat, there is, in stage 50, a complicated system of protractors and retractors of the tongue, the former consisting of genio-glossus, genio-glossus posticus externus and internus, the latter of sterno-glossus and laryngo-glossus (figs. 34-37). The sterno-glossus passes through a loop formed by a *M. annulus*. The transverse lingual fibres are not specially developed. The external pterygoid and depressor mandibulæ anterior are developed. The posterior end of the genio-hyoid is attached both to the first branchial cornu and to the thyroid cartilage. A sterno-thyroid is attached anteriorly to the posterior edge of the thyroid cartilage. The omo-hyoid, arising from the medial surface of the scapula, is in part inserted into the thyroid cartilage and in part joins the genio-hyoid.

On comparison of the above phenomena it would appear that there are two common characteristics of the jaw-muscles in Marsupials and Monotremes which may be supposed to have played a part in the phylogenetic change of an incudo-meckelian to a squamoso-mandibular joint: (1) The development of an external pterygoid. (2) The development of a (transverse) depressor mandibulæ anterior. This muscle in *Dasyurus* quickly becomes oblique and forms the anterior digastric. The condition in Monotremes, however, negatives any idea that a digastric had any share in the phylogenetic development of a squamoso-mandibular joint. In *Echidna* and Marsupials various secondary connections are developed between the elements of the hypo-branchial spinal muscles which are situated behind the first branchial bar (i. e. sterno-hyoid, omo-hyoid, and thyro-hyoid) and those in front (i. e.

¹ This account differs from that given by Fewkes in (1) the more extended posterior insertion of the genio-hyoid, (2) the existence of a sterno-thyroid, (3) the existence of an omo-hyoid—confirming the statement of Leche. The *M. annulus* was not yet separated into *M. annulus inferior* and *M. annulus intimus*.

genio-hyoid, stylo-glossus, and hyoglossus), whereby a series of long retractors of the front end of Meckel's cartilage and of the tongue are formed. Though such retractors may possibly play a part in the formation of the new jaw-joint in the individual, yet the absence of any uniformity in their development suggests that they did not do so in its phylogenetic development.

—It has generally been supposed that the formation of the new squamoso-mandibular joint was associated with the disappearance of a depressor mandibulæ. As is stated later (p. 630), there is no ontogenetic evidence of the disappearance of such a muscle, and comparison of the early stages of the hyoid muscles of Amphibia and Sauropsida with those of Mammals shows that the levator hyoidei—from which in Amphibia and Sauropsida the depressor mandibulæ is derived—preserves in Mammals, and especially in Monotremes, its primary condition as a muscle affixed to the hyoid bar.

The above considerations support the theory of Fürbringer that the change of jaw-joint was associated with the development of the mammary function: "Dieses Abweichen der Mammalia von dem fortschreitenden Entwicklungsgange, wie ihn Amphibien und Sauropsiden einschlagen, legt den Gedanken nahe, dass bei ihnen in jugendlichen Entwicklungsstadien, in den Beuteljungenkindheit, ein den Säugethieren eigentümlicher äusserer Anstoss eintrat welcher zu dieser Lockerung des Unterkiefers Veranlassung gab. Ich neige dazu, diesen in der saugenden Tätigkeit der Beuteljungen zu erblicken. Wie bei den Anurenlarven nur der vordere Teil des zu einiger Selbständigkeit gestalteten Unterkiefers zum Anheften und Kauen verwendet wurde, so dient auch bei den mammalen Beuteljungen nur der vordere Abschnitt der Mandibula der Saugfunction, welche zusammen mit der Ausbildung der Milchdrüsen eine neue Erregungsschaft gegenüber allen Nicht-Säugetieren ist."

—Some of the muscle-phenomena appear to be secondary to the change of jaw-joint. The pterygo-tympanicus of *Dasyurus* and higher Mammals becomes transformed into the tensor

veli palatini, though in *Ornithorhynchus* and some *Edentates* its ancient insertion into the tympanic bone is still preserved. The proximal end of the tensor tympani disappears and the muscle gains a new origin. The disappearance, in the ontogeny of *Dasyurus*, pig and rabbit of the *detrahens mandibulae* may also be related to the change of jaw-joint. Two slightly different views as to this muscle have been put forward. Toldt held that the muscle "bei der Neubildung des Kiefergelenkes, als ein infolge des Schwindens des *M. depressor mandibulae* notwendig gewordener Factor für die Kieferbewegung, von dem *M. masseter* abgespalten hat"; whilst Gaupp was of the opinion that it "sich zugleich mit dem *Masseter* selbst aus einer gemeinsamen Muskelmasse der Reptilien (dem sogenannten *M. capiti-mandibularis*) bei der Neubildung des Kiefergelenkes herandifferenzierte." According to both theories the muscle was developed with the new squamoso-mandibular joint. The above-recorded observations, however, suggest a converse explanation—that it is an old muscle possessed by Mammalian ancestors with an incudo-meckelian jaw-joint, which has dropped out, except in *Monotremes*, owing to its being inserted behind the new joint. The phylogenetic history would thus present an interesting contrast to that of the pterygo-tympanicus and tensor tympani.

The theory above advocated differs in some particulars from that advanced by Gaupp. In his treatise on "Die Reichertsche Theorie" it is assumed that the substitution of an incudo-meckelian jaw-joint by a squamoso-mandibular one was accompanied by a change in the masticatory muscles—from a Reptilian to a Mammalian type. The developmental phenomena occurring in the muscles, however, suggest that this substitution occurred subsequent to changes in the masticatory muscles from what may be called a pre-amphibian type, i. e. one characterised by median and lateral masticatory muscles and a levator hyoidei, to a Mammalian one.

The amount of such change is very doubtful. Possibly Mammalian ancestors with an incudo-meckelian jaw-joint

possessed internal pterygoid, a muscle representing the pterygo-tympanicus and tensor tympani (derived from the medial muscle); temporal and detrahens mandibulæ (derived from the lateral muscle); but not external pterygoid, masseter, zygomatico-mandibularis, or depressor mandibulæ anterior.

MUSCLES OF THE HYOID SEGMENT.

In stage A of the *Dasyurus* (fig. 3) the hyoid apparatus consists of hyoid and first branchial bars and a basibranchial. There is no basihyal. The ventral ends of the hyoid and first branchial bars are continuous with the basi-branchial. The hyoid bar forms a continuous structure—of stapes, inter-hyale, and stylo-hyale; the latero-hyale extends upwards from the interhyale to the auditory capsule. There is as yet no crista parotica. The only chondrified parts of the hyoid bar are the extreme lower end and the middle part; to the latter are attached the stylo-pharyngeus on the inside and the upper end of the posterior digastric on the outside. The posterior end of the stylo-glossus is attached to the tendinous part of the hyoid bar just below the middle cartilaginous part. The branchio-hyoid passes from the first branchial to the hyoid bar. The adjacent ends of the genio-hyoid, omo-hyoid and sterno-hyoid are attached to the first branchial bar. The thyro-hyoid is not yet developed. There are two hyoid muscles—the stapedius and posterior digastric. The former arises from the outer chondrified wall of the upper part of the auditory capsule and passes downwards and forwards to be inserted into the back of the upper part of the stylo-hyale. The posterior digastric takes origin from the middle chondrified — portion of the hyoid bar, and passes downward and forwards outside the bar to a transverse tendon connecting the muscle to its fellow just behind and slightly underlapping the inter-mandibularis. No trace of the anterior digastric or of the Anlage of the sphincter profundus and platysma is visible. The N. facialis passes backward on the external surface of the stapedius and then downwards on the external surface of the posterior digastric.

In stage C (figs. 7—10 and 12) the stapes¹ has chondrified. The crista parotica is beginning to form, as a slight downward extension from the chondrified portion of the outer wall of the auditory capsule. It is deepest in front, where the latero-hyale is attached, and gradually lessens behind. The stapedius muscle, taking origin from the lower edge of the crista parotica, passes forwards and downwards to the hyoid bar below the interhyale. The upper end of the posterior digastric—attached solely to the hyoid bar in stages A and B—has now an additional origin, by a long tendon passing upwards behind the hyoid bar to the paroccipital process.

In stage D (fig. 19) chondrification has extended from the middle portion of the hyoid bar into the latero-hyale, the pars inter-hyalis remaining precartilaginous. The origin of the stapedius muscle has shifted still further inwards, the muscle arising from the floor of the fossa stapedii; it is inserted into the hyoid bar below the inter-hyale.

In stage F the inter-hyale has disappeared, and the cartilaginous latero-hyale and stylo-hyale, but for a small nodule, are replaced by a ligament which, ventrally, is continuous with the cartilaginous hyoid cornu of the hyoid apparatus. The insertion of the stapedius has shifted inwards to the stapes.

In stage H the attachment of the posterior digastric to the hyoid bar is lost; its attachment to the paroccipital process is tendinous up to stage J—the latest investigated—but in the adult it has a fleshy origin.

The condition of the stapes, stapedius and posterior digastric muscles of 10 mm. specimens of *Didelphys aurita* is similar to that of the *Dasyurus* in stage H.

The anterior digastric is proliferated from the hinder part of the intermandibularis in stage D (fig. 18). The fibres are given off from the ventral surface of the posterior portion of the muscle and are directed transversely outwards, and have

¹ A stapedia artery passes through the stapes in stages A—C; it disappears subsequently.

no lateral attachment. In stage E (fig. 21) the muscle has separated from the intermandibularis; its ventral (inner) end has become attached to the ventral aponeurosis of the posterior digastric.

In stage F (fig. 22) the muscle is more obliquely situated, the muscle-fibres passing from its posterior attachment to the posterior digastric forwards and outwards to the ventral edge of the mandible. A digastric muscle is thus formed.

In an 8.5 mm. embryo of *Ornithorhynchus* (figs. 30, 31, 33), the hyoid bar, in a pre-cartilaginous condition, is a continuous structure passing from the stapedia portion above to near the middle line below. The upper, stapedia end abuts against the auditory capsule, which consists of aggregated mesoblast cells. There is no crista parotica and no latero-hyale. The hyoid muscles consist of a levator hyoidei¹ and a hyoid ventral constrictor s. styloideus, which are not quite separated from one another. The levator hyoidei has no dorsal attachment; it is inserted into the hyoid bar. The N. facialis passes backward lateral to the muscle. The hyoid ventral constrictor arises from the hyoid bar and passes down to a ventral aponeurosis connecting together the muscles of the two sides.

The hyoid muscles of *Echidna*, in stage 50 of Semon, consist of a levator hyoidei and hyoid ventral constrictor s. styloideus (fig. 37). The levator hyoidei arises from the outer end of the inturned crista parotica and is inserted into the upper end of the stylo-hyal cartilage. The hyoid ventral constrictor arises from the stylo-hyal cartilage just below the insertion of the levator hyoidei and passes downwards to a median ventral aponeurosis.

The following is a summary of Futamura's observations (1907) on the development of the hyoid muscles in the pig. In a 8.4 mm. embryo their Anlage consists of an aggregation of myogenic cells which is continuous ventrally with its fellow across the middle line. It is penetrated by the seventh nerve.

¹ The introduction of this term is explained later; the muscle is homologous with the stapedius of non-Monotreme Mammals, but never gains any insertion into the stapes.

In a 11 mm. embryo the Anlage has split into a superficial and a deep layer—the former is the Anlage of the platysma, the latter that of the stapedius, digastricus, and stylo-hyoid. In a 15 mm. embryo the antero-posterior fibres of the stapedius form the most dorsal portion of the Anlage; immediately below these is the upper end of the digastricus, i. e. this muscle has not yet extended up to the mastoid process. The digastricus is in two parts, of which the posterior (innervated by the N. facialis) is inserted into Reichert's cartilage; the anterior passes round the cartilage and is inserted in Meckel's cartilage. A small outgrowth from the posterior part is the Anlage of the stylo-hyoid. In a 21 mm. embryo the upper end of the digastricus has spread up to the mastoid process, and the jugulo-hyoideus has separated from its upper part and is inserted into the hyoid bar. The stylo-hyoid is fully separated.

Kallius (1909) described the development of some of the hyoid muscles in his account of the tongue and associated structures of the pig. In stage 12 (= Keibel's stage 22) "von dem proximalen Ende des Knorpelanlage des zweiten Schundbogen zieht ein schmaler Strang von wenig differenzierten Muskelblastem nach der Mittellinie zu in die Gegend des oralen Endes der Copula des Branchialskeletes." There is no trace of an anterior digastric. In stage 17 (= between twenty-seventh and twenty-eighth stages of Keibel) the anterior digastric forms a well "abgrenzbaren Muskelbundel welcher offenbar mit der ersten Portion (Mylohyoideus) von der ursprünglich einheitlichen Trigemini muskulatur abgezweigt hat"; its inner end is continuous by a tendon with the posterior digastric, the lower part of which is almost surrounded by the stylo-hyoid. A little higher up these two muscles diverge, the stylo-hyoid being affixed to the hyoid cartilage, the posterior digastric to the base of the skull. Both posterior digastric and stylo-hyoid receive branches from the N. facialis. (The earliest stages of development of these muscles were not described.) In stage 27 (embryo 92 mm. in greatest length) a jugulo-hyoideus is formed probably from a small part of the

posterior digastric. The stylo-hyoid has lost relation with the posterior digastric; it passes downwards, ending partially in a fascia lying at the posterior margin of the mylo-hyoid, partially by insertion into the hyoid.

Eschweiler (1911), who did not refer to the papers of Futamura and Kallius, gave an account of the development of the stapedius in the pig. He stated that the Anlage of the muscle is first visible in embryos of 13 mm. "Scheitel-Steisslänge," and has no "Abstammung von einer andern grossen Muskelgruppe." On the first development of Reichert's cartilage the muscle enters into relationship with it; it subsequently loses this and gains an attachment to the stapes. "Der Musculus Stapedius ist ein echter Abkömmling des Hyoidbogens und tritt erst sekundär mit dem Stapes, der dem periotischen Blastem entstammt, in Verbindung." The first basal attachment of the muscle is to the wall of the fossa stapedii s. Antrum petrosus laterale, and a certain rotation of the muscle takes place "in der Weise dass die Achse seiner Pyramide mit ihrem basale Ende nach hinten (aboralwärts) verschoben wird."

A re-investigation of the process of development in the pig showed the following: In a 13 mm. embryo there was no trace of an anterior digastric muscle. In a 14 mm. embryo it is being proliferated from the ventral surface of the hinder part of the intermandibularis, but is not separated from it, whilst the muscle Anlagen in the hyoid segment show the same structure as in the 15 mm. stage. In a 15 mm. embryo (figs. 55, 56) the anterior digastric is a little separated from the intermandibularis; it extends backwards and upwards on the lateral surface of the hyoid ventral constrictor portion of the muscle Anlagen in the hyoid segment, to about its middle. In the hyoid segment the hyoid bar consists of a continuous stapes, inter-hyale, and stylo-hyale (figs. 55-57) in a precartilaginous condition, and the latero-hyale extends upwards from the junction of the inter-hyale and stylo-hyale towards the auditory capsule, which shows no trace of a fossa stapedii or crista parotica. The muscle-Anlagen (figs. 56-58), not yet

separated into stapedius and hyoid ventral constrictor, extend as a continuous strip from behind the latero-hyale downwards and forwards lateral to the stylo-hyale, and then anterior to the stylo-hyale to the middle line just behind the posterior edge of the intermandibularis.

In a 17 mm. embryo the anterior digastric is quite separated from the intermandibularis. The stapedius portion of the hyoid muscle-Anlage is partially separated from the hyoid ventral constrictor, and some of its fibres are inserted into the back of the upper end of the stylo-hyale.

In a 19 mm. embryo the crista parotica is formed and the upper end of the latero-hyale is continuous with it. The stapedius muscle is now quite separated from the hyoid ventral constrictor; it arises from the floor of the fossa stapedii and is inserted into the inter-hyale. The hyoid ventral constrictor has no dorsal attachment, its upper end lies just below the stapedius, and it extends downwards to a ventral aponeurosis. The anterior digastric extends laterally to Meckel's cartilage, whilst posteriorly it extends backwards and upwards on the lateral surface of the hyoid ventral constrictor, as in the 15 mm. stage.

In a 21 mm. embryo (figs. 61-63) the inter-hyale has disappeared and the stapedius is inserted into the stapes. The hyoid ventral constrictor has extended dorsally and its upper end is attached to the paroccipital process, and it has divided into dorsal and ventral portions. The dorsal portion is partially separated into jugulo-hyoideus and posterior digastric. The jugulo-hyoideus is inserted into the stylo-hyal cartilage. The lower end of the posterior digastric is continuous with the posterior end of the anterior digastric. The anterior end of the anterior digastric is attached laterally to the Anlage of the mandible. The dorsal end of the ventral portion of the hyoid ventral constrictor is attached to the stylo-hyale; from this point it passes downwards to the transverse ventral aponeurosis.

In a 24 mm. embryo the only change is a slightly greater separation of the jugulo-hyoideus and posterior digastric. In

a 32 mm. embryo (fig. 64) the ventral end of the lower part of the original hyoid constrictor has gained an insertion to the external surface of the first branchial cornu, though keeping its transverse aponeurosis to the muscle of the opposite side—a stylo-hyoid muscle is thus formed.

The developmental phenomena in the rabbit are, for the most part, similar to those in the pig. The anterior digastric is proliferated from the intermandibularis, and grows backwards medial (not lateral, as in the pig) to the hyoid ventral constrictor. The latter divides into dorsal and ventral portions, the dorsal of which separates into posterior digastric and jugulo-branchialis, whilst the ventral forms the stylo-hyoid. The jugulo-branchialis becomes inserted into the first branchial cornu; and the stylo-hyoid into the basibranchial, losing its ventral transverse aponeurosis. The posterior digastric becomes tendinous.

On the Primary Form of the Posterior Digastric in Mammals.—Bijvoet's conclusion, from an examination of the adult condition of the stylo-hyoid and posterior digastric in many classes of Mammals, was that, primitively, "sich vom Schädel zum Zungenbein, oder besser zu einer Bindegewebslager, das sich ventral am Hyoid heftet, eine Muskelmasse erstreckt, die vom N. facialis innerviert wird." "Den hier beschriebenen Zustand begegnen wir bei *Echidna* und *Ornithorhynchus*. Der *M. styloideus* repräsentiert die einheitliche Muskelmasse, welche vom Schädel entspringt und die ventrohyoideale Bindegewebsmasse sich festheftet."

The developmental phenomena in *Ornithorhynchus*, *Echidna*, *Dasyurus*, pig, and rabbit show that a still more primitive condition of the muscle is one in which it is attached dorsally to the hyoid bar and passes ventrally to a transverse aponeurosis, forming a hyoid ventral constrictor or interhyoideus. This condition in *Dasyurus*, pig and rabbit is succeeded by one in which the muscle loses its dorsal attachment to the hyoid bar, and, extending dorsally, gains a new one to the skull—to either the paroccipital or mastoid process. The more primitive condition, however, persists in *Echidna*,

in which animal Toldt described the *M. styloideus*¹ as arising from the stylo-hyale close to its cranial end.² This I can confirm (vide fig. 38); it arises from the upper end of the stylo-hyale and from the latero-hyale, lapping round the insertion of the levator hyoidei.³

Comparison of this adult condition with stages 47 and 50 (fig. 37) shows that the origin of the muscle has spread slightly up the hyoid bar. The muscle also arises from the stylo-hyale in *Manis pentadactyla* (fig. 43).

It is doubtful whether this primitive condition exists in any Mammals other than these two. It is true that Kohlbrugge described the posterior belly of the digastricus as arising from the styloid process in the Marsupials, *Cuscus orientalis* and *maculatus*, *Paradoxurus hermaphrodita*, and *Macropus brunii*. But in *Cuscus maculatus*, Bijvoet described and figured the posterior digastric as arising from the paroccipital process—an occurrence which suggests that in the specimen examined by Kohlbrugge the condition was one of division of a posterior digastric s. hyoid ventral constrictor into dorsal and ventral portions (vide pp. 617, 618), of which only the ventral was described. The same explanation possibly applies to the other Marsupials described by Kohlbrugge.

→ A condition intermediate between that of *Echidna* and the usual one of attachment to the skull is present in *Ornithorhynchus*, where Toldt described the muscle as arising from the stylo-hyale and hinder wall of the cartilaginous external auditory meatus.⁴

¹ I employ the nomenclature of Schulman. Toldt names the muscle the "stylohyoideus,"—a terminology suggesting a homology with the "stylohyoideus" of the pig and rabbit, which is developed from the ventral part only of the hyoid ventral constrictor (vide pp. 617, 618).

² Bijvoet described the muscle as arising "unmittelbar hinter dem äusseren Gehörgange."

³ No representative of a possible upper portion of the muscle was present.

⁴ Bijvoet described it as arising "von der Schädelbasis und empfängt accessorische Ursprünge vom äusseren Gehörganges." Schulman did not state its origin.

→ The hyoid ventral constrictor or styloideus muscle, unconnected with the anterior digastric to form a digastricus, passes downwards to a ventral aponeurosis connecting it with its fellow below the basibranchial and ventral ends of the hyoid bars. This condition is present in stages A-D of *Dasyurus*, in 14 mm. embryos of the pig, and is preserved to the adult condition in *Echidna* and *Ornithorhynchus* (Schulman), and in *Manis*. It is also present in some of those Edentates, i. e. *Dasypus villosus*, *Tolypentes tricinatus*, and *Tatusia novemcincta* (Toldt), in which a sterno-mandibularis exists. The latter muscle (vide p. 625) is formed by the union of the anterior digastric with the sterno-hyoid, and the transverse aponeurosis of the hyoid ventral constrictor s. posterior digastric lies dorsal to the longitudinal muscle.

In some Edentates, e. g. *Bradypus tridactylus*, the anterior end of the sterno-hyoid is in part attached to the posterior edge of the transverse aponeurosis of the hyoid constrictor s. posterior digastric (Bijvoet).

In some Edentates the hyoid ventral constrictor s. styloideus s. posterior digastric divides into dorsal and ventral portions, the former taking origin from the skull and inserted into the stylo-hyal, the latter arising therefrom and passing to a ventral aponeurosis.

Thus in *Bradypus tridactylus* (Bijvoet) the posterior digastric arises from the mastoid process and passes to a ventral aponeurosis (fig. 40)¹; whilst in *Bradypus marmoratus* (fig. 41) the muscle is divided into dorsal and ventral portions. The stapedius muscle is present. A similar condition was found in a 30 mm. embryo, though the separation into dorsal and ventral portions was not quite complete.

Toldt described the posterior digastric in *Dasypus villosus* as arising from the mastoid; its tendon broadens and unites with the posterior border of the mylo-hyoid. In *Dasypus novemcincta* (embryo 30 mm.) the posterior digastric is partly divided into dorsal and ventral portions,

¹ This figure of Bijvoet is reproduced for comparison with one of *Bradypus marmoratus*.

inserted into and arising from the stylo-hyale (fig. 42). A stapedius of usual origin and insertion is present.

Mackintosh described the posterior digastric of *Choloepus* as arising from the stylo-hyale, but did not mention the existence of any muscle arising from the mastoid and inserted into the bar. Such a muscle, however, is pictured in a figure of Schulman under the title of mastoideo-hyoideus.

Toldt stated that the posterior digastric was absent in *Tamandua*, but described and pictured a "stylo-hyoideus," innervated by the N. facialis, taking origin from the os tympanicum and inserted into the cranial end of the hyoid cornu, and also described a portion of the intermandibularis as arising from the hyoid cornu. These two muscles are in all probability the dorsal and ventral portions of the posterior digastric. This identification is rendered all the more certain by his statement that there is an anastomosis between the mylohyoid branch of the fifth and the seventh nerves.

Owen described three muscles in *Myrmecophaga jubata*—a "stylohyoideus" passing from the petro-hyoid to the stylo-hyale, a "cerato-hyoideus" passing from the cerato-hyale to a commissural tendon with a slip to the sternomandibularis muscle, and a "constrictor salivaris" passing from the cerato-hyale downwards over the salivary reservoir to the commissural tendon and blending with the back of the intermandibularis. It is probable from his description and figures that his "stylo-hyoideus" and "cerato-hyoideus" are the dorsal and ventral portions of a divided posterior digastric. Leche stated that the constrictor salivaris is innervated by the N. mylo-hyoideus and is to be regarded as a differentiated part of the intermandibularis.

The condition of the hyoid ventral constrictor is thus variable in Edentates, even in closely related species. Thus it is undivided in *Bradypus tridactylus*, divided into upper and lower parts in *Bradypus marmoratus*; undivided in *Dasypus villosus*, divided in *Dasypus novemcincta*. And in at least one Marsupial—*Cuscus maculatus*—the condition is variable within the same species (vide p. 619).

A sterno-mandibularis may occur with either condition, e. g. with an undivided hyoid ventral constrictor in *Tolypentes tricinctus* and *Dasypus villosus*, with a divided one in *Dasypus novemcincta*, *Myrmecophaga* and *Tamandua*.

In the pig, as described above, the hyoid ventral constrictor divides into dorsal and ventral portions. The dorsal portion separates into two muscles—the jugulo-hyoideus and the posterior digastric. The jugulo-hyoideus is inserted into the stylo-hyal. The ventral end of the posterior digastric unites with the posterior end of the anterior digastric and forms the digastric muscle. The ventral portion of the hyoid ventral constrictor becomes the stylo-hyoid; it arises from the stylo-hyal and passes to a ventral aponeurosis uniting it with its fellow, and also gains an insertion to the side of the first branchial cartilage.

In the rabbit the sequence of events is, but for two differences, the same. The jugulo-hyoideus gains an insertion to the first branchial cartilage, becoming the jugulo-branchialis. The ventral portion of the constrictor becomes the stylo-hyoid and is inserted into the basibranchial; the ventral aponeurosis disappears.

In both animals the posterior digastric becomes tendinous and has no nerve-supply, but in the embryo a branch of the N. facialis nerve passes to it.

On the Formation of the Anterior Digastric Muscle.—Consideration of the adult form and innervation of the anterior digastric muscle led Gegenbaur, Ruge, Fürbringer, Schulman and Bijvoet to the opinion that it is derived from the intermandibularis s. mylo-hyoid, and the observations of Kallius, though he did not observe the earliest stages of the process, tended to confirm this view. Chaine stated that the digastric muscle is due to longitudinal division of a muscle extending from the sternum to the mandible into inner and outer portions, the inner forming the genio-hyoid and sterno-hyoid, the outer the digastricus.

Futamura stated that in man and pig the anterior digastric is due to a forward extension to the jaw of the muscle blastema

which gives rise to the stapedius, stylo-hyoid, and posterior digastric. This forward growth receives a secondary innervation from the fifth nerve. These statements were adversely criticised by Bijvoet.

The above-recorded observations show that the depressor mandibulæ anterior of *Ornithorhynchus*, and its homologue, the anterior digastric of *Dasyurus*, pig and rabbit, are formed by proliferation from the ventral surface of the intermandibularis.

On the Formation of the Digastric Muscle.—Schulman, followed by Bijvoet, came to the conclusion that the primitive condition of the anterior digastric muscle is indicated by the depressor mandibulæ anterior of *Echidna* and *Ornithorhynchus*,¹ viz. a sheet of approximately transverse fibres below the intermandibularis, attached laterally to the lower jaw; that this transverse sheet became more longitudinal in direction, and that its hind end—the original inner end—gained an attachment to the transverse aponeurosis of the posterior digastric muscle. A condition similar to that of *Bradypus tridactylus* would result, and from this all the varied forms of a digastricus verus and digastricus spurius can be easily derived.

Toldt's theory of the phylogenetic development of the digastricus muscle differs from that of Schulman and Bijvoet in some particulars, and is as follows. The anterior digastric "besitzt ursprünglich, gleich dem *M. mylohyoideus*, den Character und die Bedeutung eines Eingeweidemuskels; er ist die äussere Langsfaserschichte des Mundhöhlenbodens, angelegt der Querfaserschichte desselben, dem *M. mylohyoideus*." This longitudinal muscle unites with a hinder longitudinal muscle innervated by the twelfth, to form a continuous longitudinal muscle—the sterno-mandibularis, extending from the sternum to the lower jaw. This condition is

¹ Schulman, "führt die Vereinigung des *M. depressor mandibulæ* anterior mit vom *N. facialis* versorgten *M. depressor mandibulæ* posterior oder richtiger einem hyoidealen Componenten des *M. constrictor* zur Bildung eines wirklichen *M. digastricus*."

present in *Myrmecophaga*, *Tatusia*, *Dasypus villosus*. In *Tolypeutes tricinctus* a tendinous inscription is present between the anterior and posterior portions, and is attached to the hyoid. A sterno-hyoideus lies dorsal to the posterior portion. The posterior digastric ends in a transverse aponeurosis in intimate connection with the posterior margin of the intermandibularis. In *Bradypus tridactylus* there is a tendinous inscription; the anterior portion forms an anterior digastric and the posterior portion a true sterno-hyoideus in that whilst its median portion is attached to the inscription its lateral portion is attached to the first branchial bar. The posterior digastric is attached to the lateral end of the inscription. A digastric muscle is thus formed. This condition is one intermediate between those described above and that found in higher Mammals.

The following observations bear on this question. In embryos of Amphibia and Sauropsida, and also in the rabbit and pig, the hypobranchial spinal muscles—formed by downgrowths from two or more anterior body myotomes—form a longitudinal cell column, the anterior end of which, growing forward dorsal to the inter-hyoideus, s. hyoid ventral constrictor and intermandibularis to the front end of Meckel's cartilage, divides into two at the level of the second or first branchial cartilage, the part in front forming the genio-hyoid, the part behind the sterno-hyoid. In the rabbit and pig this primitive sterno-hyoid develops into sterno-hyoid, sterno-thyroid, thyro-hyoid, omo-hyoid.¹

It would follow that any connection of the anterior end of the sterno-hyoid with a muscle lying ventral to the intermandibularis s. mylohyoid is a secondary phenomenon.

Further, in a 30 mm. embryo of *Dasypus novemcinctus* the following condition was found: The sterno-mandibularis had a tendinous intersection at the level of the hind edge of the intermandibularis. The sterno-thyroid was attached to the basibranchial and thyroid cartilage by two separate slips. A thyro-hyoid extended from the thyroid to the first branchial

¹ Details of this development will be given in a later paper.

bar. The genio-hyoid and hyo-glossus arose from the basi-branchial and first branchial bar and extended forward to the anterior end of the lower jaw and tongue respectively. A branchio-hyoid s. cerato-hyoid muscle, between the first branchial and hyoid bars, was also present. The posterior digastric consisted of upper and lower parts, the upper extending from the mastoid to the hyoid bar, the lower from the hyoid bar to an aponeurosis immediately behind and continuous with the intermandibularis. A stylo-glossus arose from the hyoid bar.

In this specimen, then, there was evidence of fusion between a sterno-hyoid and anterior digastric to form a sterno-mandibularis. In the other Edentates possessing a sterno-mandibularis Toldt does not state whether the muscle was investigated microscopically.

These phenomena tend to show that the connection of the sterno-hyoid to the transverse aponeurosis of the posterior digastric is a secondary phenomenon and related to its non-attachment to the first branchial bar, and suggest that its fusion with the anterior digastric to form a sterno-mandibularis is also related to the same occurrence.

The theory of Toldt, again, quite fails to account for the fact that in *Dasyurus* the anterior digastric, when first formed, grows out transversely just as in *Ornithorhynchus*, and only subsequently takes up a longitudinal direction.

The theory of Toldt is thus open to many objections, and may probably be rejected in favour of that of Schulman and Bijvoet.

The above observations, however, show that there are two main varieties of a digastric muscle in mammals.

(1) The anterior digastric becomes connected with the ventral end of the hyoid ventral constrictor s. stylo-hyoideus; no stylo-hyoid muscle is present. This occurs in Marsupials and those Edentates in which a digastric is formed. There are two sub-varieties: (a) the hyoid ventral constrictor remains undivided in most Marsupials and some Edentates, e.g. *Bradypus tridactylus*; (b) the hyoid ventral con-

strictor divides into dorsal and ventral portions, and the anterior digastric becomes connected with the lower end of the ventral portion, e. g. *Bradypus marmoratus*, *Cholæpus*, and probably the Marsupials examined by Kohlbrugge (vide p. 619).

(2) The hyoid ventral constrictor divides into dorsal and ventral portions, and the anterior digastric becomes connected with the lower end of the dorsal portion; the ventral portion forms, as a rule, the stylo-hyoid muscle. This condition is present in all Eutheria. Phylogenetically, it is probably derived from sub-variety (b) above, rather than from sub-variety (a). Such a digastric muscle may be of many different forms—classified by Bijvoet into “*digastricus verus*” and “*digastricus spurius*.”

The posterior digastric of this latter class of Mammals is partially or wholly—according to whether a mastoideo- s. jugulo-hyoideus s. jugulo-branchialis is or is not developed—homologous with the dorsal portion of the posterior digastric of these Edentates, in which division into dorsal and ventral portions takes place. The mastoideo- s. jugulo-hyoideus preserves the ancient insertion of the muscle. The stylo-hyoideus is homologous with the ventral portion. It may pass to the middle line and join its fellow, thus preserving the primitive condition, as in *Cynocephalus* (Bijvoet); or, keeping the transverse aponeurosis it may gain an additional insertion to the branchial cornu, as in the pig; more commonly, however, the aponeurosis disappears and the muscle is inserted into the basibranchial or its branchial cornu, as in the rabbit. The origin of the muscle often extends upwards on the stylo-hyal and may even reach the skull, so that it is overlapped by the posterior digastric, and the primitive positions of the two muscles are obscured.

According to Bijvoet a stylo-hyoid muscle is absent in *Erinacæus* among Insectivora, the Cheiroptera, and some Mustelidæ, but he also states that in some *Erinacæus* some bundles of the posterior digastric stream to a thin membrane which passes inwards to the middle line ventral to the hinder

part of the mylo-hyoid, whilst in Cheiroptera and Mustelidæ some of the hinder bundles of the mylo-hyoid arise from the hyoid. A representative of the ventral part of the hyoid constrictor is thus present, though not forming a stylo-hyoid muscle.

In view of these phenomena of comparative anatomy and embryology it is probable that the accounts given by Rouvière and Futamura of the development of the stylo-hyoid of man—that it is an outgrowth of the posterior digastric—are in need of revision.

On the Reported Instances of a Monogastric Digastric Muscle Inserted into the Lower Jaw.—Kohlbrugge found this condition present in one specimen of *Hystrix* with a fifth nerve innervation, and found a two-bellied condition in another specimen. The former was explained by Schulman as one in which an anterior digastric had extended backwards.

In *Manis javanica* Kohlbrugge described the digastric as a simple muscle extending from the “hinteren Schädelseite zum Kieferwinkel,” whilst in *Manis macrura* Windle and Parsons found the digastric “inserted into the lower jaw as far as halfway to the symphysis.” In *Manis pentadactyla* (fig. 43) there is a muscle, with the insertion described by Windle and Parsons, arising partly from the mastoid and partly by fibres which are continuous with the platysma in the neck, i.e. an auriculo-mandibularis. The posterior digastric is present—in the form of a hyoid ventral constrictor, arising from the stylo-hyal and innervated by the N. facialis; its anterior edge, ventrally, is continuous with the posterior edge of the intermandibularis. The anterior digastric muscle is absent.

In *Tatusia* and *Dasypus* a monogastric muscle, attached below to the mandible, was described by Macalister, but later investigations by Toldt show that a posterior digastric passing to a ventral aponeurosis is present, so that the first described muscle is an auriculo-mandibularis.

In *Orycteropus*, Humphry described the digastric as

extending "from mastoid process to angle and lower margin of jaw." Subsequently, Chaîne stated that "au lieu du muscle que signale Humphry j'ai trouvé une formation mi-tendineuse mi-musculaire qui parassait en tenir lieu," probably, therefore, an auriculo-mandibularis; and he also depicted, though not describing, an additional muscle named digastric.

It is not known whether a true posterior digastric exists in *Cyclothurus* and *Chlamydophorus*. In the latter a small muscle passing from the bulla tympani to the mandible was found by Macalister, but not by Hyrtl.

The case of *Tamandua* is considered above (p. 621).

The existence of a monogastric muscle homologous with the posterior digastric and inserted into the lower jaw is thus very doubtful. The instances which have been described are probably cases of an auriculo-mandibularis—which is derived from the platysma (vide pp. 632, 634).

On the Primary Form of the Stapedius Muscle in Mammals.—The stapedius muscle in early post-embryonic stages of *Dasyurus* arises from the outer surface of the auditory capsule and is inserted into the upper part of the stylohyale, forming a levator hyoidei. Its origin subsequently shifts to the lower edge of the developing crista parotica, and then to the floor of the fossa stapedii, whilst its insertion shifts to the stapes. The initial stage present in *Dasyurus* is, in part, passed over in the rabbit and pig, for in them the first dorsal attachment of the muscle is to the floor of the fossa stapedii; on the other hand, its first ventral attachment is to the upper end of the stylo-hyale, subsequently shifting to the inter-hyale and then to the stapes as in *Dasyurus*. The shifting of insertion from the inter-hyale to the stapes takes place with the disappearance of the inter-hyale in all three animals. The primary form of the stapedius as a levator hyoidei is present in 8.5 mm. embryos of *Ornithorhynchus*, and in stage 47 of *Echidna*, and in them persists into adult life. It is the muscle which was termed "mastoideo-hyoideus" by Schulman and Bijvoet.

This identification affords an explanation of the statements of Huxley, Eschweiler and Fürbringer, that a stapedius muscle, i. e. one of the usual mammalian type, is absent in Monotremes, and also of the method of innervation. In non-Monotreme Mammals the nerve to the stapedius is given off from the N. facialis proximal to the chorda tympani. Now in *Echidna*—according to Schulman—the mastoideo-hyoideus is innervated by several fine twigs from the N. facialis, some of which are given off proximal to, and some with, the chorda tympani.

The relations of the N. facialis to the levator hyoidei s. stapedius in *Echidna* are different from those in *Ornithorhynchus*, *Dasyurus*, pig and rabbit. In the latter four animals the nerve passes backwards lateral to the muscle and then downwards. Earlier stages of *Ornithorhynchus* and *Dasyurus* were not available, but in the rabbit and pig this condition is preceded by one in which the nerve passes outwards dorsal to the Anlage of the stapedius and hyoid ventral constrictor and then downwards. The levator hyoidei s. stapedius thus extends upwards on the inner, medial, side of the nerve to gain a dorsal attachment to the outer surface of auditory capsule or to the floor of the fossa stapedii.

In stage 47 of *Echidna* the nerve passes backwards in the sulcus facialis dorsal to, and separated by the incurving crista parotica from the levator hyoidei which arises from it. In stage 50 (figs. 36 and 37) the origin of the levator hyoidei has extended outwards to the base of the crista parotica, and in the adult (fig. 38) to the outer surface of the auditory capsule. The N. facialis consequently passes backwards medial to the muscle, whereas in other Mammals it passes backwards lateral to it.

It would thus appear that the name "mastoideo-hyoideus" has been applied by various investigators to three muscles of differing origin and morphological nature: (1) to a stapedius muscle which has preserved a levator hyoidei stage, as in Monotremes; (2) to the dorsal portion of a hyoid ventral constrictor which has divided into dorsal and ventral portions,

as in *Bradypus marmoratus*, *Dasypus novemcincta*, *Cholœpus didactylus*; and (3) to the part of the dorsal portion of a hyoid ventral constriction which is inserted into the stylo-hyal, as in the pig.

The name "stylo-hyoideus" was applied by Owen and by Toldt to (2) above, and also by Toldt to the hyoid ventral constrictor of Monotremes.

On the Homologies of the Posterior Digastric Muscle in Non-Mammals.—According to Gegenbaur and Ruge the posterior digastric is homologous with the depressor mandibulæ of lower vertebrates, and the latter thought that the change of insertion, from mandible to hyoid, was related to the formation of the new squamoso-mandibular joint. Fürbringer and Bijvoet rejected this theory, the former being of opinion that the old depressor mandibulæ was either altogether gone or would be found as a rudimentary structure attached to the malleus, the latter finding it difficult to understand how the insertion of a depressor mandibulæ should be transferred to the hyoid.

Bijvoet's theory was that the posterior digastric is derived from a ventral constrictor of the hyoid segment, and is serially homologous with the intermandibularis s. mylohyoid of the mandibular segment. This becomes all the more probable from the investigations detailed in this paper, which show that the primary upper attachment of the muscle is to the hyoid bar.

The serial homology is well brought out in fig. 4, which, being drawn from a slightly oblique section of *Dasyurus* in stage B, shows the posterior digastric on one side and the intermandibularis on the other.

On the Homologies of the Stapedius in Non-Mammals.—Fürbringer was of the opinion that the depressor mandibulæ of non-mammals has entirely disappeared in mammals, or will be found as a rudiment attached to the malleus—the hind end of the primitive jaw. No such rudiment, however, was found in the embryos investigated.

Gaupp stated that the disappearance of the depressor is a

fact: "Der Schwund des alten *M. depressor mandibulæ* bei den Säugern und damit der Wechsel in dem Muskelmechanismus bei den Oeffnung des Mundes sind Tatsachen."

But, perhaps, after all, the muscle has not disappeared. It has been shown above that the stapedius muscle of Mammals is primarily a levator hyoidei arising from the outer wall of the auditory capsule and inserted into the upper part of the hyoid bar. Now, the depressor mandibulæ of Dipnoi, Urodela¹ and Sauropsida, as I have shown in a former paper, is at first a levator hyoidei inserted into the hyoid bar—a condition which persists in Protopterus—and only subsequently becomes attached to the hind end of Meckel's cartilage. It may be inferred that the stapedius muscle of Mammals is homologous with the levator hyoidei of Urodela and Sauropsida though not with its later stage of depressor mandibulæ—there being no developmental or other evidence that it ever gained that secondary attachment.

The origin of the superficial facial and platysma muscles has been investigated by the methods of comparative anatomy and by direct observation of the phenomena of development.

Rabl stated that the platysma develops in the territory of the hyoid arch, grows forward, and upwards behind the Anlage of the external ear, and gives rise to the whole of the mimetic facial musculature and that of the epicranium. He did not further particularise exactly where and how it develops, nor the relationship of the Anlage of the platysma to the stapedius, posterior digastric and stylo-hyoid.

Futamura stated that in man and pig the facialis musculature is derived from an aggregate of myogenic cells round the motor facial nerve. The proximal part consists of two layers separated by the *N. facialis*, of which the lateral forms the *Platysma colli*.

There is no trace of the superficial facial and platysma

¹ The condition in the Anura is more complicated, the levator hyoidei of the tadpole forming only the superficial portion of the depressor mandibulæ of the adult form.

muscles in Stages A and B of *Dasyurus*. Indifferent mesoblast cells lie between the lateral surface of the hyoid ventral constrictor and the epidermis (fig. 5). In stage C (fig. 13) the Anlage of the sphincter profundus and platysma muscles is developed in this mesoblast, about midway between the lateral surface of the hyoid ventral constrictor and the epidermis, and extending dorsally lateral to the submaxillary gland. No evidence is afforded by the sections that these embryonic muscles are proliferated or delaminated from the hyoid ventral constrictor—they are developed in the sub-epithelial mesoblast. In stage D (fig. 18) the embryonic muscle-cells are better developed and have spread forwards into the mandibular segment. In stage E (figs. 20 and 21) they have spread still further forwards in the mandibular segment, and down the neck. In the mandibular and hyoid segments they show evidence of division into two layers—an inner, of cells elongated in the transverse plane, the sphincter profundus; and an outer, of cells elongated in the longitudinal plane, the platysma. In stage F (figs. 22 and 23) these two sheets are more widely separated, and the platysma has spread dorsally over the temporal muscle and forwards, forming the Anlage of the sphincter palpebrarum; whilst the sphincter profundus does not extend dorsally above the level of the zygomatic arch. The sphincter profundus is not developed behind the external ear; its hindmost fibres form the depressor auris s. pars auricularis of the constrictor profundus. The Anlage of the auriculo-mandibularis is formed as a forward and downward growth from the platysma sheet, opposite the incus (fig. 23). In stage H (fig. 28) and in the 10 mm. stage of *Didelphys aurita* (fig. 39) it has separated from the platysma and extended forwards and backwards; its anterior end is attached to the posterior edge of the mandible and its posterior end to the internal surface of the aural cartilage.

In stage H the buccinator and maxillo-labialis are formed from the sphincter profundus.

The muscles of the external ear begin to be differentiated

in stage F, and are well marked in stage H; the depressor auris, as stated above, is developed from the sphincter profundus; all the other muscles are developed from the platysma sheet, which is solely present behind the ear, and in front solely present above the zygomatic arch. They consist of sculutaris, post-auricularis, auriculo-occipitalis, three little muscles on the outside, and two—the transversus and obliquus—on the medial side of the cartilage.

These developmental phenomena in *Dasyurus* confirm the opinion of Boas and Paulli that the orbicularis palpebrarum is derived from the platysma sheet, the opinion of Ruge that the buccinator is derived from the sphincter profundus, and show that the maxillo-labialis is derived from the sphincter profundus.

In an 8.5 mm. embryo of *Ornithorhynchus* the Anlage of the sphincter superficialis and platysma muscles is present in the hyoid segment outside the hyoid ventral constrictor (figs. 29-33). It has spread forwards into the mandibular segment, and backwards into the neck. It shows slight indications of separating into the sphincter superficialis and platysma sheets.

In 14 mm. embryos of the pig there is no trace of the Anlage of the sphincter profundus and platysma muscles; the space between the outer surface of the Anlage of the stapedius and hyoid ventral constrictor and the epiblast is packed with mesoblast, in which no trace of differentiation can be seen. In 15 mm. embryos (figs. 56, 58) the Anlage of the sphincter profundus and platysma can be seen in the ventral part of the hyoid segment, close to the epiblast, and separated by an interval filled with indifferent mesoblast cells from the Anlage of the hyoid ventral constrictor.

The auriculo-mandibularis muscle—either muscular or tendinous—is present in many Mammals. It takes origin from the cartilaginous portion of the external auditory meatus or cartilage of the outer ear, and is inserted into the ramus ascendens of the mandible (Bijvoet). It is innervated by the N. facialis, either by a branch from the rami auriculares

posteriores, e. g. *Canis* (Chaine), or by a more distal branch than that for the posterior digastric, e. g. *Tatusia*, Marsupials (Bijvoet).

Two views have been advanced as to the derivation of the muscle. Chaine held that it is homologous with the depressor mandibulæ of lower Vertebrates; Fürbringer and Bijvoet that it is a derivation of the facial musculature. The above-described phenomena in *Dasyurus* prove the correctness of the latter theory; they show that it is derived from the platysma. The muscle is one which was identified by some observers as a single-bellied digastric inserted into the lower jaw, e. g. in *Dasyurus*, *Tatusia*, *Manis*. This question is discussed above (pp. 627, 628).

On the Derivation of the Muscles of the External Ear.—The comparative anatomy of the muscles of the external ear in Mammals has been investigated by Ruge, Baum and Kirsten, and by Boas and Paulli; their development by Killian, Dobers and Futamura.

Ruge was of the opinion that all the auricular muscles were derived from the platysma; none from the sphincter profundus.

Boas and Paulli agreed with this opinion, except in regard to the depressor auris, which they described as the pars auricularis of the sphincter profundus.

Killian stated that the muscles in front of the ear—*attraheus*, *attolens* (anterior part), *helicis major*, *helicis minor*, *tragicus*—were derived from an upgrowth of the platysma in front of the ear; and those behind—*retrahens*, hinder part of the *attolens*, *obliquus*, *transversus*—from the hinder superficial layer of the dorsal portion of the hyoid arch musculature.

Dobers stated that in the pig the muscles develop from two groups which “*zwar gemeinschaftlicher Abstammung sind, sich jedoch sehr frühzeitig trennen.*” One group lies from the very beginning caudo-dorsal to the ear; the second group lies more ventral, and can be called the embryonic platysma, for it also gives rise to the platysma myoides.

From the second group develop the trapezius, adductor auris inferior and externus and helix major; from the first group the other muscles.

Futamura's statements differ much from the above; they are that, in the pig, the scutularis, helix major and minor are developed from the platysma, and the other muscles from the sphincter auris, which is derived from the sphincter colli.

In *Dasyurus* the superficial muscle sheet spreads upwards from the site of its formation in the mesoblast external to the hyoid ventral constrictor, and divides into two layers, each consisting of embryonic muscle-cells easily distinguishable from one another and from surrounding mesoblast. The sphincter profundus does not spread above the zygomatic arch, nor is it present behind the ear. Only the depressor auris is developed from the sphincter profundus; all the other muscles are derived from the platysma sheet. This method is also evident in *Didelphys aurita*. The embryological phenomena in these two Marsupials thus confirm the theory of Boas and Paulli.

The development of the cervical portion of the platysma by gradual descent from the hyoid region is of special interest owing to the discovery by Kohlbrugge that in many Marsupials and Edentates¹ the R. cervicis of the N. facialis is entirely replaced by the Nn. cutanei of the cervical nerves so that it is entirely restricted to the face. Kohlbrugge advanced the following theories in explanation: "Entweder täuscht der R. colli des Menschen nur eine primitive Lage vor und erreichte die Halsregion nur durch ein Herabrücken der Muskulatur welches bei den Marsupialieren dann noch nicht bei den Monotremen wohl eingetreten wäre, oder wir müssen eine secundäre Reduction dieser Theile bei Marsupialiern (und Manis) annehmen, die Gegend welche sonst der Facialis-muskulatur angehörte wäre dann von den spinalen Nerven und ihrer Muskeln erobert worden." He was inclined to accept the latter theory.

¹ *Cuscus orientalis*, *Cuscus maculatus*, *Paradoxurus hermaphrodita*, *Macropus brunii*, *Manis javanica*.

There is a third possibility—that the superficial muscles of the neck may be of facial origin and receive a secondary innervation by cervical nerves; this is confirmed by the developmental phenomena in *Dasyurus*, where the platysma originates in the hyoid region and spreads down the neck.

This phenomenon is one which can be assimilated with others occurring in the muscles of the head. I have previously given a list of thirteen in various Vertebrates, which appear to be referable to the law that if a muscle grows into one or more neighbouring segments, that portion tends to be innervated by the corresponding nerve or nerves.

It is noteworthy that in Monotremes (McKay, cited by Kohlbrugge) the cutaneous muscles of the neck are innervated by both the N. facialis and the first four cervical nerves—i. e. a condition exists re innervation intermediate between that present in Marsupials and that in which the innervation is solely by the seventh nerve. It is similar to the double innervation of the trapezius by the N. accessorius and cervical nerves.

Kohlbrugge also found that in Marsupials the cervical nerves innervate the Platysma sheet in front of the ear, the N. facialis only innervating the sphincter profundus. The cervical nerves thus spread beyond their segmental territory and innervate muscles which did not originate in it. This must be a very rare occurrence as regards motor nerves, though it is paralleled by the N. vagus.

On the Homologies of the Sphincter superficialis s. colli, Platysma, and Sphincter profundus, in Non-Mammals.—Ruge, who investigated the adult form of the hyoid muscles in all classes of Vertebrates, stated that the sphincter colli of Monotremes is homologous with the muscle C_2 vd of Selachians, and the Platysma group with the muscle C_2 md.

Now in *Ornithorynchus*, *Dasyurus* and pig these muscles are formed from a common Anlage developed in the mesoblast outside and not as an extension backwards of the hyoid ventral constrictor—so that the homologies suggested by Ruge

appear impossible. Similarly, they cannot be homologous with the constrictor colli of Sauropsida, for this is developed as an extension backwards of the levator hyoidei and inter-hyoideus, nor with the backward extension of the inter-hyoideus which occurs in many Amphibia.

It is therefore doubtful whether these skin muscles of Mammals have any homologies in non-mammals; they have probably been developed within the Mammalian phylum.

The phenomena recorded above suggest (1) that the sphincter profundus, platysma, and sphincter superficialis muscles have been developed within the Mammalian phylum. (2) That the other muscles developed in the hyoid segment are derived from (a) a levator hyoidei, arising from the outer surface of the auditory capsule and inserted into the upper part of the hyoid bar; (b) a ventral constrictor or inter-hyoideus, arising from the hyoid bar and passing to a median raphe.

When the primitive conditions of the mandibular and hyoid muscles in Mammalia are compared with those of Amphibia and Sauropsida, it becomes clear that they point to the same conclusion as that arrived at by Fürbringer in his "Abstammung der Säugethiere"—that Mammals are descended from a pro-amphibian stock.

I have, in conclusion, to offer many thanks to Prof. J. P. Hill for the loan of sections of *Dasyurus viverrimus* and *Ornithorhynchus*, to Prof. W. N. Parker for the loan of sections of an adult *Echidna*, to Dr. Assheton for the loan of specimens of *Echidna* (stages 47 and 50) and *Phascolarctos*, to Herbert Donnison, Esq., for the head of a *Phoca vitulina*, to Fraulein Snethlage for an embryo and head of an adult *Bradypus marmoratus*, and to the Director of the Calcutta Museum for the head of a *Manis pentadactyla*.

The expenses of the work and its publication have been defrayed by a grant from the Committee of the Bristol University Colston Society.

September 2nd, 1913.

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EXPLANATION OF PLATES 38-45,

Illustrating Dr. F. H. Edgeworth's paper "On the Development and Morphology of the Mandibular and Hyoid Muscles of Mammals."

ABBREVIATIONS.

Ala temp. Ala temporalis. *alisphen. b.* Alisphenoid bone. *An. hy. gloss. & styl. gloss.* Anlage of the hyo-glossus and stylo-glossus muscles. *An. pal. & pty. b.* Anlage of palate and pterygoid bones. *An. of intermand. m.* Anlage of intermandibularis muscle. *An. of mast. ms.* Anlage of masticatory muscles. *An. par. b.* Anlage of parietal bone. *An. Sph. sup. & platys.* Anlage of sphincter superficialis and platysma muscles. *An. stap. & hy. v. cons.* Anlage of stapedius and hyoid ventral constrictor. *An. tens. pal. & tens. ty.* Anlage of tensor veli palatini and tensor tympani muscles. *An. zygo. & mass.* Anlage of zygomatico-mandibularis and masseter muscles. *Annulus m.* Annulus muscle. *ant. dig. m.* Anterior digastric muscle. *aud. cap.* Auditory capsule. *aud. epith.* Epithelium of auditory vesicle. *aur. mand. m.* Auriculo-mandibularis muscle. *aur. temp. n.* Auriculo-temporal nerve. *basibr. c.* Basibranchial cartilage. *1 br. bar.* First branchial bar. *br. hy. m.* Branchio-hyoid muscle s. cerato-hyoideus s. inter-hyoideus. *br. IX to g. s. p.* Branch of ninth nerve to great superficial petrosal nerve. *bucc. m.* Buccinator muscle. *buccal n.* Buccal nerve. *chorda ty.* Chorda tympani nerve. *com. br. IX to VII.* Communicating branch of ninth nerve to seventh nerve. *cons. ph. m.* Constrictor pharyngis muscle. *crista par.* Crista parotica. *cut. br. mylohy. n.* Cutaneous branch of the mylohyoid nerve. *dep. auris m.* Depressor auris muscle. *dep. mand. ant. m.* Depressor mandibulae anterior muscle. *detr. mand. m.* Detrahens mandibulae muscle. *E. A. M.* External auditory meatus. *ext. pty. m.* External pterygoid muscle. *ext. rect. m.* External rectus muscle of eye. *Eust. th.* Eustachian tube. *Gass. g.* Gasserian ganglion. *gen. gloss. m.* Genio-

glossus muscle. *gen. gloss. post. ext.* Genioglossus posticus externus muscle. *gen. gloss. post. int.* Genioglossus posticus internus muscle. *gen. hy. m.* Genio-hyoid muscle. *genic. g.* Geniculate ganglion of seventh. *g. s. p.* Great superficial petrosal nerve. *ham.* Hamulus. *hy. ep. m.* Hyo-epiglotticus muscle. *hyogloss. m.* Hyo-glossus muscle. *hy. v. cons.* Hyoid ventral constrictor muscle. *hy. v. cons. d. p.* Hyoid ventral constrictor muscle, dorsal portion. *hy. v. cons. v. p.* Hyoid ventral constrictor muscle, ventral portion. *inf. d. ling. & mylohy. n.* Trunk which divides into inferior dental, lingual and mylo-hyoid nerves. *int. car. a.* Internal carotid artery. *int. hyal.* Inter-hyale. *interart. men.* Interarticular meniscus of jaw joint. *intermand. m.* Intermandibularis muscle. *int. pty. m.* Internal pterygoid muscle. *jug. hy. m.* Jugulo-hyoideus muscle. *lam. asc. a. t.* Lamina ascendens alæ temporalis. *lary. gloss. m.* Laryngo-glossus muscle. *lat. hyal.* Latero-hyal cartilage. *lat. m.* Lateral masticatory muscle. *lev. hy. m.* Levator hyoidei muscle. *lev. pal. m.* Levator veli palatini muscle. *ling. n.* Lingual nerve. *ling. & chorda ty.* United lingual and chorda tympani nerves. *ling. br. IX.* Lingual branch of ninth. *mal. b.* Malar bone. *mall.* Malleus portion of Meckel's cartilage. *Mam. pty. b.* Mammalian pterygoid bone. *mand.* Mandible. *mass. m.* Masseter muscle. *mass. n.* Masseter nerve. *max. b.* Maxilla bone. *Me.* Meckel's cartilage. *med. m.* Median masticatory muscle. *memb. ob.* Membrana obturatoria. *mid. cerv. v.* Middle cervical vein. *Mon. pty. b.* Monotreme pterygoid bone. *mylohy. n.* Mylo-hyoid nerve. *otic. g.* Otic ganglion. *orb. par. com.* Orbito-parietal commissure. *pal. b.* Palate bone. *pal. ns.* Palatine nerves. *par. b.* Parietal bone. *platys. m.* Platysma muscle. *phar.* Pharynx. *post. dig. m.* Posterior digastric muscle. *post. dig. m. d. p.* Posterior digastric muscle, dorsal part. *post. dig. n. v. p.* Posterior digastric muscle, ventral part. *presph. c.* Presphenoid cartilage. *premand. s.* Premandibular segment. *proc. alaris.* Process alaris. *pty. bo.* Pterygoid bone. *r. lat. V₂.* Ramus lateralis of the mandibular division of fifth. *r. med. V₂.* Ramus medialis of the mandibular division of fifth. *sph. prof.* Sphincter profundus. *sph. sup.* Sphincter superficialis. *sphen. pal. g.* Spheno-palatine ganglion. *sq. b.* Squamous bone. *stap. m.* Stapedius muscle. *sternogloss. m.* Sterno-glossus muscle. *sternohy. m.* Sterno-hyoid muscle. *st. mand. m.* Sterno-mandibularis muscle. *st. mast. m.* Sterno-mastoid muscle. *stylogloss. m.* Stylo-glossus muscle. *stylyal.* Stylo-hyal cartilage. *stylph. m.* Stylo-pharyngeus muscle. *styloid. m.* Styloideus muscle s. hyoid ventral constrictor. *sub. max. gl.* Submaxillary gland. *temp. m.* Temporal muscle. *tend. post. dig.* Tendon of posterior digastric muscle. *tend. tens. pal.* Tendon of tensor veli palatini muscle. *tens. pal. m.* Tensor veli palatini muscle. *tens. ty. m.* Tensor tympani muscle. *thyrohy. m.* Thyro-hyoid muscle. *thyro. cart.* Thyroid cartilage. *trap. m.* Trapezius muscle. *tym. b.* Tympanic bone. *vid. n.* Vidian nerve.

zygo. mand. m. Zygomatico-mandibularis muscle. Roman numerals. Cranial nerves.

Dasyurus viverrimus, figs. 1-28.

Figs. 1-3.—From transverse sections, stage A (just born; greatest length, in spirit, 5.5 mm., head length 2.5 mm.); fig. 1 is the most anterior. Fig. 1, slide 1, row 1, number 17; fig. 2, s. 1, r. 7, n. 3; fig. 3, s. 1, r. 8, n. 12.

Fig. 4.—From transverse section, stage B (few hours old; greatest length 5.75 to 6 mm., head length 3 mm.): the section is a little oblique and the right side is anterior to the left; s. 2, r. 1, n. 1.

Fig. 5.—Portion of transverse section, stage B; s. 2, r. 1, n. 20, showing undifferentiated mesoderm between posterior digastric muscle and epiblast.

Figs. 6-10.—From sagittal sections stage C (twenty-six hours old; greatest length 6 mm., head length 3.25 mm.); fig. 6 is the most anterior. Fig. 6, s. 1, r. 2, n. 1; fig. 7, s. 1, r. 3, n. 6; fig. 8, s. 1, r. 4, n. 1; fig. 9, s. 1, r. 4, n. 7; fig. 5, s. 1, r. 5, n. 9.

Fig. 11.—From transverse section stage C; s. 2, r. 2, n. 15.

Fig. 12.—Portion of transverse section, stage C, s. 2, r. 3, n. 8, showing stapedius muscle.

Fig. 13.—Portion of transverse section, stage C, s. 2, r. 4, n. 11, showing Anlage of sphincter profundus and platysma muscle.

Figs. 14-18.—From transverse sections, stage D (probably three days old; greatest length 7 mm., head length 4 mm.); fig. 14 is the most anterior. Fig. 14, s. 1, r. 8, n. 1; fig. 15, s. 1, r. 8, n. 9; fig. 16, s. 1, r. 8, n. 13; fig. 17, s. 2, r. 1, n. 3; fig. 18, s. 2, r. 2, n. 4.

Fig. 19.—Portion of transverse section, stage D, s. 2, r. 3, n. 12, showing stapedius muscle.

Figs. 20, 21.—From transverse sections, stage E (5 or 6 days old; greatest length 8 mm., head length 4.5 mm.); fig. 20 is the more anterior; Fig. 20, s. 2, r. 4, n. 12; fig. 21, s. 2, r. 5, n. 5.

Figs. 22, 23.—From transverse sections, stage F (about 7 days old; greatest length 8.5 to 9 mm., head length 5 to 5.5 mm.); fig. 22 is the more anterior. Fig. 22, s. 2, r. 8, n. 10; fig. 23, s. 3, r. 2, n. 13.

Figs. 24-27.—From transverse sections, stage H (about 14 days old; greatest length 13.5 mm., head length 8 to 8.5 mm.); fig. 24 is the most anterior. Fig. 24, s. 5, r. 3, n. 10; fig. 15, s. 5, r. 5, n. 2; fig. 26, s. 5, r. 6, n. 8; fig. 27, s. 6, r. 2, n. 10.

Fig. 28.—From transverse section, stage J (25 days old; greatest length 20 mm., head length 12.5 mm.); s. 3, r. 2, n. 5.

Ornithorhynchus, figs. 29-33.

Figs. 29-31.—From longitudinal sections, embryo 8.5 mm.; fig. 29 is the most lateral. Fig. 29, s. 3, r. 2, n. 4; fig. 30, s. 4, r. 1, n. 3; fig. 31, s. 4, r. 3, n. 4.

Figs. 32, 33.—From transverse sections, embryo 8.5 mm.; fig. 32 is the more anterior. Fig. 32, s. 8, r. 1, n. 12; fig. 33, s. 7, r. 1, n. 3.

Echidna, figs. 34-38.

Figs. 34-37.—From transverse sections, 25 mm. long (= stage 50 of Semon); fig. 34 is the most anterior.

Fig. 38.—From transverse section, young adult 12.5 cm. long.

Fig. 39.—Transverse section, *Didelphys aurita*, 10 mm.

Fig. 40.—Sketch copied from Bijvoet, showing digastric muscle of *Bradypus tridactylus*.

Fig. 41.—Sketch showing digastric muscle of *Bradypus marmoratus*.

Fig. 42.—From transverse section, *Dasypus novemcincta*, 30 mm.

Fig. 43.—Sketch of side of head of *Manis pentadactyla*.

Fig. 44.—Sketch of muscles on inside of jaw of *Phoca vitulina*.

Rabbit, figs. 45-54.

Fig. 45.—Transverse section, embryo 5½ mm. crown-rump length.

Figs. 46-48.—Transverse sections, embryo 16 mm. crown-rump length; fig. 49 is the most anterior.

Figs. 49-53.—Longitudinal horizontal sections, embryo 23 mm. crown-rump length; fig. 54 is the most dorsal.

Fig. 54.—Longitudinal horizontal section, embryo 33 mm. crown-rump length.

Pig, figs. 55-64.

Figs. 55-58.—Transverse sections embryo 15 mm. crown-rump length; fig. 60 is the most anterior.

Fig. 59-63.—Transverse sections, embryo 21 mm. crown-rump length; fig. 68 is the most anterior.

Fig. 64.—Transverse section, embryo 32 mm. crown-rump length.

TEXT-FIGURES.

Figs. 65-67.—Sketches of model of developing masticatory muscles of rabbit, embryo 13 mm. crown-rump length; fig. 65 from inside, fig. 66 from front, fig. 67 from outside.

Figs. 68, 69.—Sketches of model of developing masticatory muscles of rabbit, embryo 16 mm. crown-rump length; fig. 68 from inside, fig. 69 from outside.

Figs. 70, 71.—Sketches of model of developing masticatory muscles of pig, embryo 19 mm. crown-rump length; fig. 70 from inside, fig. 71 from outside.

Figs. 72, 73.—Sketches of model of developing masticatory muscles of pig, embryo 21 mm. crown-rump length; fig. 72 from inside, fig. 73 from outside.

Figs. 1-28, 39-41, 43 were drawn by Mr. E. E. Shellard.

Figs. 65-73 were drawn by Mr. C. W. Sharpe.